

A Morphological Study of Imagine Heliconiinae (Lep.: Nymphalidae) with a Consideration of the Evolutionary Relationships within the Group^{1,2}

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(Plate I; Maps 1-17; Text-figures 1-153)

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[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," by William Beebe, *Zoologica*, 1952, Vol. 37, No. 13, pp. 157-184].

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I. INTRODUCTION AND ACKNOWLEDGMENTS

RESEARCH on the Heliconiinae by both amateur and professional lepidopterists reached its first peak around the turn of the last century. The group was popular, not only because of the exhibition of brilliant colors which made for spectacular collections, but also because of a surge of interest in the biological problems posed by polymorphism and what has been interpreted as intra- and inter-generic mimicry.

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Jocelyn Crane, the Director of the New York Zoological Society's Department of Tropical Research, has been responsible more recently for the promotion of a program of research on the Heliconiinae which has included studies on rearing technique (Crane & Fleming, 1953), the morphology of the eggs, larvae and pupae (Fleming, 1960; Beebe, Crane & Fleming, 1960), larval and pupal behavior and biology (Alexander, 1961a, b), spectral reflectance of wings (Crane, 1954), imaginal behavior (Crane, 1955, 1957), occurrence and genetics of imaginal polymorphism (Beebe, 1955; Turner & Crane, 1962; Sheppard, 1963), and on palatability and Müllerian mimicry (Brower, Brower & Collins, 1963).

The purpose of this paper is to compare the morphology of the adult butterflies and estimate the proximity of the evolutionary relationships among them. It is fortunate that Trinidad has six of the seven genera recognized by Michener (1942a) and that the nine local species of *Heliconius* are drawn from nine of the twenty-one infra-generic groups erected by Stichel & Riffarth in 1905. H. Martin Brown³ is currently making a revision of *Heliconius* so the only species of that genus included in this study are the nine species that occur in Trinidad, though some aspects of *H. telesiphe* are considered as it appears to be biologically associated with *Podoricha telesiphe*.

These boundaries have been defined to avoid overlap with subsequent publications on the genus *Heliconius* and to present a paper which will be complete for use in Trinidad.

In the course of this work the collections of Heliconiinae in the museums of the eastern United States, England and Paris were examined, and field work was undertaken in Colombia and eastern and western Ecuador as well as in Trinidad. The support of the National Science Foundation and the University of the West Indies made possible the trips to North and South America.

The author is grateful to Jocelyn Crane for stimulating interest in this topic, to Julie Emsley for the drawings, and to the trustees and staff of the British Museum (Natural History), the American Museum of Natural History, the United States National Museum, the Museum of Comparative Zoology at Harvard University, the Hope Department of Zoology at Oxford, the University Museum of Cambridge and the Paris Museum of Natural History, for study facilities and the loan of material.

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II. SYSTEMATIC SYNOPSIS, WITH SPECIAL REFERENCE TO DISTRIBUTION

In 1827, Swainson (Philos. Mag. Ser. 2, 1:187) proposed a new family, the Nymphalidae, one of whose constituent subfamilies was the "Heliconiinae." He limited the Heliconiinae to *Heliconius* in the strict sense, though subsequent authors included firstly *Eueides* (e.g., Stichel & Riffarth, 1905) and later Michener (1942a) included species previously allocated to the genera *Colaenis*, *Philaethria*, *Dione* and *Agraulis*.

The rather superficial characters given by Doubleday & Westwood (1846) and Stichel & Riffarth (1905) are not peculiar to the group nor do they allow the inclusion of genera other than *Heliconius*. Characters of value are, cell R of the forewing (discal cell) always closed, the basal branch of Sc of the hindwing recurrent and unforked, androconia always present on two or more wing veins, odiferous glands developed between segments eight and nine in females. The larvae are typically nymphalid (Fracker, 1915) and feed on various species of *Passiflora* (Passifloriaceae).

The group has been given status varying from tribe (Zerny & Beier, 1936) to full family (Stichel & Riffarth, 1905), but when their characters are considered within the framework of the Nymphalidae, subfamily is the upper acceptable limit.

Though primarily endemic to the neotropics, where they occur on both sides of the Andes and in the east extend as far as 35° South, they are also incursive in the Nearctic region and in exceptionally warm summers may reach as far as 50° North, although 36° North is their normal limit. Their range also includes the Bahamas Islands, Bermuda, the Greater and Lesser Antilles and the Galapagos Islands.

The maps not only reflect the distribution of the insects but also the itineraries of collectors. Most noticeable is the apparent dearth of Heliconiinae from the savannas of the Matto Grosso and Goliás of Brazil. This could be a real phenomenon due to the vegetation and climate, or could be due to inaccessibility to collectors, though there are a few localities within this area where *Dryas iulia* and *Heliconius aliphera* are known. Seaport localities are suspect as they may be only the ports of exit of collectors or collections. Personal experience in the Andes has shown that the mountain cities like Bogotá, Quito and Ambato are usually the localities of the hotels in which the collectors stayed and give no indication whether the insects were taken on the eastern or western slopes. In most cases the authentic localities are sparsely distributed and

do not allow the boundaries of species or subspecies to be defined with accuracy. Lists of acceptable localities taken from specimens in the museums mentioned in the acknowledgments have been deposited with each museum.

Important taxonomic papers for the group are Stichel (1903 and 1938), Stichel & Riffarth (1905), Neustetter (1929) and Michener (1942a).

Philaethria dido (Clerck)

(Text-figs. 4, 23, 44, 62, 87, 98, 107, 124, 142, 153; Map 1; Pl. I, Fig. 5)

Philaethria Billberg 1820, Monobasic, Enum. Ins. in Mus. Bibg., p. 77.

Genotype: *Papilio dido* Clerck 1764, designated by Scudder 1875, Proc. Amer. Acad. Arts Sci., 10:248.

= *Metamandana* Stichel 1907, Gen. Ins., fasc. 63, p. 6, pl. 1, figs. 1, 2, 3a and 3b.

= *Metamorpha* (part) Hübner 1818, Verz. bekannt. Schmett., p. 43.

Philaethria dido (Clerck 1764), as *Papilio dido*, Icones, Sect. 2, Register pl. 30.

This large black and green butterfly (see Seitz, 1913, pl. 84a) extends from 17° North in Guatemala through Central America to South America east of the Andes at lat. 28° South. Its apparent absence from the llanos of Venezuela and the savannas of eastern Brazil is possibly real, for it normally inhabits the upper canopy and margins of rain forests. On the other hand it is easily overlooked, as it flies high and is very hard to catch. There are no records west of the Andes, which is surprising for though it is rarely found above 800 metres, it does occur in northern Colombia. There is a specimen in the M.C.Z. labelled "Cuba cl. Wright," but though the species is alleged to have occurred in Hispaniola, Bates (1935) doubted its authenticity. However de la Torre y Callejas (1949) reported a specimen being seen in Havana province. The sexes are alike. Variation between specimens from any one locality is almost as great as between specimens from the extremities of its range, and moreover, even in life, the green ground color fades rapidly. It is presumably the capture of specimens of different ages which has led to the description of forms such as *Metamorpha dido* var. *ostara* Rober 1906 (Soc. Ent., 20: 177) from Cauca which is alleged to be pale and large, and *Metamandana dido diatonica* Fruhstorfer 1912 (Ent. Rdsch., 29: 14-15) from Honduras (B.M. 1937-285) which is alleged to be smaller, but neither of these can be regarded as good subspecies. There are, however, two clearly distinguishable forms which are regarded here as subspecies, though there are data in museum collections which suggest

that they can occur sympatrically. The known localities for each form are included on the distribution map. More detailed and accurate data are required to clarify the position.

There seem no good grounds for suggesting that *P. dido* and *Victorina steneles* form a mimetic pair, for though in museum collections they are somewhat similar, in life their habitats rarely overlap, though their territory could be covered by a single avian predator. Their habits make each clearly recognizable to human observers.

Philaethria dido dido (Clerck 1764)

The typical form occupies the whole range of the species with the possible exception of some of the southern localities.

Philaethria dido wernickei (Rober 1906)

as *Metamorpha wernickei*, Soc. Ent., 20:177. [B. M. 1937-285, Obidos],

= *Metamorpha dido pygmaeon* Fruhstorfer 1912, Ent. Rdsch., 29:14.

In this variety both sexes lack the rust-colored markings on the underside of the wings. It appears to occur sympatrically with typical *dido* south of the Amazon and is possibly a genetic polymorph. It is unfortunate that no series of specimens is known from one locality, by one collector, which contains both forms. Museum collections do not normally warrant quantitative consideration, but the relative abundance of *wernickei* seems to increase towards the southern limits of the species and Hayward (1952) states that it is the only form known from northern Argentina, though there are Paris museum records of *dido dido* from near Rio de Janeiro and Rio Grande do Sul. The specimen in the Hope collection labelled "Bogotá" is probably in error, for not only is the altitude excessively high but Dr. E. Schmidt-Mumm⁴, a contemporary resident and experienced collector in Colombia, has never seen it.

Dryadula phaetusa (Linnaeus)

(Text-figs. 3, 24, 45, 69, 88, 94, 104, 106, 125, 145, 153; Map 2; Pl. I, Fig. 3)

Dryadula Michener 1942, Monobasic, Amer. Mus. Novit. No. 1197, p. 4, figs. 5 and 10.

Genotype: *Papilio phaetusa* Linnaeus 1758.

= *Colaenis* Hübner 1819 (part), Verz. bekannt. Schmett., p. 32.

Dryadula phaetusa (Linnaeus 1758), as *Papilio (nymphalis) phaetusa*, Syst. Nat. (10 ed.) 1, p. 478.

This large orange and black butterfly (Seitz, 1913, pl. 84c) extends from Mexico at 23° North, and Florida (Martin & Truxal, 1955)

⁴Dr. E. Schmidt-Mumm, Optometra, Bogotá, Colombia.

through Central America to South America, where on the eastern side of the Andes it extends as far as 35° South and on the western side at least as far south as Guayaquil. Over its whole range it is very local, rarely occurring above 800 metres and seems to prefer open damp low-lying land. Its absence from the Amazon Basin and the dry savannas of eastern Brazil is not unexpected in view of its ecological preferences elsewhere, but the full extent of its range may not be known yet, on account of its normally restricted localities, fast erratic flight and the paucity of collections from some areas. Males can be distinguished from females by the more orange ground color and the more intense and precise dark markings. Variation within specimens from any one locality is nearly as great as the variation within the whole range of the species, so no good geographical subspecies can be distinguished. This variability has in the past led to the description of such forms as *D.p. stupenda* Stichel 1907 (as *Colaenis phaetusa* forma *stupenda*, Gen. Ins. fasc. 63, p. 13) from Panama, which has a particularly red ground color, and *deleta* (♂) and *lutulenta* (♀) which were described from Paraguay by Stichel in the same paper as having more dull coloration.

Agraulis vanillae (Linnaeus)

(Text-figs. 5, 38, 39, 61, 68, 81, 97, 108, 132, 151, 153; Map 3; Pl. I, Fig. 2)

Agraulis Boisduval & Le Conte 1836, Monobasic, Hist. Gen. Lèp. Chen. Amér. Sept., p. 142-43.

Genotype: *Papilio vanillae* Linnaeus 1758, = *Dione* Hübner 1818 (part), Verz. bekannt. Schmett., p. 31.

Agraulis vanillae (Linnaeus 1758), as *Papilio (nymphalis) vanillae* Syst. Nat. (10 ed.), 1. p. 482.

In exceptionally warm years this orange and black butterfly (Seitz, 1913, pl. 84f) ranges from British Columbia at lat. 50° North, but more normally from 36° North on both sides of the continent, through the southern States to Central America, and through the Bahamas and the Greater and Lesser Antilles to South America. It reaches 33° South on the eastern side of the Andes and at least as far as Lima (12° South) on the western side. It seems limited to altitudes below 1,500 metres. There are no records from the savannas of eastern Brazil in spite of the fact that elsewhere it is a common and conspicuous butterfly which is easy to catch. It usually inhabits forest margins and open scrub or young secondary growth forests. The review of the subspecies by Michener (1942b) is accepted and followed here.

Subspecies (1) *Agraulis vanillae vanillae* (Linnaeus 1705), as *Papilio vanillae* figured in Merian, Metam. Ins. Surinam, p. 25, pl. 25.

The typical subspecies occurs from eastern Panama throughout the whole of South America east of the Andes as far as about 20° South and it also occurs in Trinidad, Tobago, Barbados, Grenada, the Grenadines, St. Vincent and St. Lucia, where it grades into *A. v. insularis*, which is the characteristic form of the Greater and northern Lesser Antilles. It has also been recorded from Bermuda, but since *insularis* is naturally nearer, it was probably transported on a ship or plane.

Subspecies (2) *Agraulis vanillae insularis* Maynard 1889, as *Agraulis insularis* Contrib. Sci. Philad. Acad. Sci., 1:89.

With the type locality "Bahama Island," the range of this variable subspecies includes Nassau, Andros and New Providence (Michener 1942b), North and South Bimini (Rindge 1952), Exuma Cay, Wandereck Well Cays, Staniard Cay, Little and Great Farmers Cay, Derby Island, Cat Island, Great Inagua, West Caicos, Grand Turk, Cay 3.5 miles S.W. of N. Caicos, Maniguana Island, Crooked Island, Long Island, San Salvador Island, Fortune (Long Cay), Fish Cay, Dead Mans Cay, Eleuthera Island, Berry Island, Albow Cay, Abaco Cay, Great Abaco and Grand Bahama (Rindge 1955); Cuba, Jamaica, Grand Cayman, Cayman Brac, Little Cayman, Hispaniola, Puerto Rico, St. Croix, St. Thomas, St. Bartholomew, St. John, St. Kitts, Montserrat, Anguilla, Guadeloupe, Dominica and Martinique. This form can be distinguished with certainty from typical *vanillae* from the southeastern Antilles only when long series of specimens are compared. It may not breed on all islands from which it is recorded, for this butterfly is capable of considerable flights over water, as evidenced by a British Museum specimen taken at sea south of Panama at lat. 6°44' N. by long. 79°26' W., that is 75 miles from the nearest land. It is interesting to notice how *A. vanillae*, though variable in the Antilles, has not differentiated into forms comparable with those of *Dryas iulia*.

Subspecies (3) *Agraulis vanillae nigrior* Michener 1942, Amer. Mus. Novit. No. 1215, p. 7.

This subspecies occurs in the southeastern United States and in exceptional summers as far north as New York, but usually from North Carolina through South Carolina, Georgia, Alabama to Florida and its Keys, and westward through Tennessee, Mississippi, Louisiana, Arkansas and Missouri where it intergrades with *incarnata*. The distinction between the Greater Antillean *insularis* is clear, even though

separated by only 75 miles of water. De la Torre y Callejas (1949) records a specimen taken from Cuba in 1945, but which is surely an immigrant. Gunder (1929, Bull. Brooklyn Ent. Soc. (n. ser.) 24: 327, p. 31, fig. 7) described a melanic variety from Ontario as *hewlettae*. The life history in the southern States has been studied by Randolph (1922).

Subspecies (4) *Agraulis vanillae incarnata* (Riley 1926), as *Dione vanillae incarnata*, Entomologist, 59:243.

This subspecies, whose type locality is Durango City, Mexico, has in exceptional years been taken as far north as British Columbia and Wisconsin, but its more normal distribution is from California at lat. 37° North through Arizona, New Mexico and Texas to Mexico and Central America as far as Panama. Wright (1896) maintained that its range was extended north through California when the Southern Pacific Railroad was opened in 1885. Gunder described a number of aberrant melanic varieties under the infra-subspecific names *comstocki* (1925, Ent. News Philad., 36: 5, pl. 1, fig. T), *fumosus* (1925, Ent. News Philad., 33: 137, pl. 2, fig. 9) and *marginapertus* (1928, Canad. Ent. 60: 163, pl. A, fig. 3a), all from Los Angeles.

Subspecies (5) *Agraulis vanillae forbesi* Michener 1942, Amer. Mus. Novit. No. 1215, p. 3.

This subspecies with the type locality of Lima forms the southern limit of the species on the western slopes of the Andes and in northwestern Colombia it grades into typical *vanillae*.

Subspecies (6) *Agraulis vanillae galapagensis* Holland 1889, in Howard, Proc. U. S. Nat. Mus., 12:194.

This distinct subspecies is confined to the Galapagos Islands from which it has been recorded on Chatham (type locality), Albemarle, James, Charles and Indefatigable Islands. Some specimens of *forbesi* are very similar in size, pattern and color but differ in that the forewing spots which lie antero-distal to the discal cell are not contiguous, as they are in *galapagensis*. Doubtless it is from a population on the Peruvian coast that the Galapagos Islands have been colonized.

Subspecies (7) *Agraulis vanillae maculosa* (Stichel 1907), as *Dione vanillae maculosa*, Gen. Ins. fasc. 63, p. 18.

This subspecies is characteristic of the southeastern regions of the Andes and occurs as far south as Uruguay and northern Argentina. It has also been recorded from Chile at Limache but this seems very unlikely to be natural, for it is on the western slopes. Towards the north in Brazil this form grades into typical *vanillae* but in the northwest towards the tributaries of

the Upper Amazon, though there are few records, it seems to grade through *catella* to *lucinia*. The form *superargentata* described by Giacomelli (1925, Rev. Chil. Hist. Nat., 29: 228) has not been seen.

Subspecies (8) *Agraulis vanillae lucinia* C. and R. Felder 1862, as *Agraulis lucinia* Wein. Ent. Monatschr., 6:110.

The status of this very distinct form is still in doubt, for though it appears to be confined to the tributaries of the Upper Amazon at a higher altitude than typical *vanillae* there is insufficient field data to be sure that they do not occur sympatrically. Apart from color and pattern, *lucinia* is morphologically indistinguishable from other forms of *vanillae* and the existence of individuals intermediate in color and pattern like *catella* demonstrates that it is not completely reproductively isolated. The variable form *catella* was described by Stichel in 1907 (as *Dione vanillae catella*, Gen. Ins. fasc. 63, p. 18) and is known only by a small number of specimens.

Agraulis vanillae varies over its range principally in size and the development of the dark markings, and considering the substantial seasonal variation in specimens from any one locality and the similarity of trend in specimens from localities with similar climatic conditions the main causes of these differences may be environmental, though there is no experimental evidence. The form *lucinia* differs substantially from the remainder of the subspecies in the consolidation of the dark markings, and the reduction of silver spots which produces an effect very similar to that of *Dione juno*, with which it is grossly sympatric. There is no evidence that there is a mimetic association between *A. lucinia* and *D. juno* though the similarity is remarkable. It is unfortunate that the range of *lucinia* is in one of the least-collected areas of the continent and it is not known whether *lucinia* in the field flies with either *D. juno* or other forms of *vanillae*. However, the differentiation of *lucinia* is complex enough to assume that it is a genetic variety and not an environmental form.

Dione Hübner

Dione Hübner 1818, Verz. bekannt. Schmett. p. 31.
Genotype: *Papilio juno* Cramer 1779, designated by Scudder, 1875, Proc. Amer. Acad. Arts Sci., 10:157.

Dione juno (Cramer)

(Text-figs. 11, 34, 35, 58, 63, 84, 96, 109, 129, 148, 153; Map 4; Pl. I, Fig. 1)

Dione juno (Cramer 1779), as *Papilio juno*, Pap. Exot., 3:38, pl. 215, figs. B and C.

This orange and black butterfly (Seitz, 1913, pl. 84e) occurs from Mexico at lat. 28° North through Central to South America, where on the east of the Andes it extends as far as lat. 35° South and on the west as far as southern Peru at lat. 17° South. It is allegedly known from Hispaniola and there is one unconfirmed record from Cuba (Hall, 1925). In the Lesser Antilles it is known only from the islands south of and including Martinique. The sexes differ in that the females are usually larger. In habits, habitats and continental distribution it is very similar to *Agraulis vanillae*.

Subspecies (1) *Dione juno juno* (Cramer 1779), as *Papilio juno* (*loc. cit.*).

The typical subspecies occurs in South America and is generally distributed from north-western Colombia, where it grades to the north into *huascama*, throughout the whole of South America east of the Andes as far as 35° South, and includes the islands of Trinidad, Tobago, Grenada, the Grenadines, St. Vincent, St. Lucia and Martinique. Throughout its range it is very uniform and the sexes are similar. Hayward (1931, Rev. Soc. Ent. Argent., 4: 40) described *suffumata*, which has not been seen. It is doubtful if it normally occurs above 1,500 metres. The early stages have been studied by d'Almeida (1944). The absence of records from the savannas of eastern Brazil is probably real, for it is usually a common insect where it occurs at all and is easy to catch.

Subspecies (2) *Dione juno huascama* (Reakirt 1866), as *Agraulis huascama*, Proc. Acad. Nat. Sci. Philad., pp. 243-244.

This subspecies ranges from northern Mexico at lat. 28° North through Central America to Colombia where east of the Magdalena Valley it grades into *juno*. It differs from the typical form in that it is larger, usually paler, with the dark border to the posterior margin of the hindwing spotted with ground color, and is more variable. Sexual dichromatism is pronounced, the females being lighter in color, and with the dark markings less precise. Rarely above 1,500 metres.

Subspecies (3) *Dione juno andicola* (Bates 1864), as *Agraulis andicola*, Journ. Ent., 2:187.

This subspecies extends from western Colombia along the western slopes of the Andes below 2,200 metres, through Ecuador to southern Peru at lat. 17° South. It differs from *huascama* principally in its smaller size, and in that the dark markings of both sexes are paler. The early stages have been studied by Brown (1944). A specimen from Lima shows typical *juno* markings but may have been taken on the eastern slopes. The form *miraculosa* described by Hering from Huacho, Peru (1926, Deutsch Ent. Zeit.

Ivies, 40: 196-201, figs. 2 & 5), has not been seen.

Dione moneta Hübner

(Text-figs. 9, 37, 60, 82, 111, 128, 149, 153; Map 5)

Dione moneta Hübner (& Geyer) 1825, figured in Samml. Exot. Schmett. 2, pl. 20, figs. 1 & 2.

This orange and black butterfly (Seitz, 1913, pl. 84e) ranges from Mexico at lat. 25° North through Central and South America east of the Andes as far as 30° South. On the western slopes it occurs at least as far as 3° South. The sexes are similar.

Subspecies (1) *Dione moneta moneta* Hübner 1825 (*loc. cit.*).

The typical subspecies forms the southern extremity of the range extending northwards from latitude 30° South as far as about 20° South, where in Bolivia it grades into *butleri*, from which it may be distinguished by its smaller size and medium sized spots of ground color on the posterior border of the hindwing. It has not been recorded from central or eastern Brazil so it appears to be confined to the eastern slopes and foothills of the Andes. The early stages have been studied by Brown (1944).

Subspecies (2) *Dione moneta butleri* Stichel 1907, Gen. Ins., fasc. 63, p. 19.

This form intergrades with *moneta* around 20° South and extends northwards along the eastern slopes of the Andes into *poeyii*. Specimens taken from the western slopes of the Andes are intermediate between *butleri* and *poeyii* in that they are medium sized but have the spots on the posterior border of the hindwing intermediate between the small ones characteristic of *butleri* and the large ones of *poeyii*. There is a record by Wallengren (1863) of a specimen from the Galapagos Islands, but even if correct then it is certainly not established there now.

Subspecies (3) *Dione moneta poeyii* Butler 1873 as *Dione poeyii*, Ann. Mag. Nat. Hist. (ser. 4), 12:227.

This northern subspecies ranges from about lat. 27° North, where on occasions it has been recorded from Texas, through Mexico and Central America to Panama. It can be distinguished by the larger size and by the very large spots of ground color on the posterior border of the hindwing.

Over-all there is a north-south cline of decreasing size and darkening of posterior border to the hindwing, a tendency which is reversed slightly at the southern extremity of the range. Hall (1921) is of the opinion that it does not often occur below 1,000 metres in Central America and it has certainly attained 3,500 metres in Costa Rica. From locality data and

field observations this may be true over its whole range and explains the similarity between the forms taken on both sides of the Andes. The map shows only the gross range within which it may be expected to occur, for museum localities are sparse.

Dione glycera (C. & R. Felder)

(Text, figs. 10, 36, 59, 64, 83, 110, 127, 150, 153; Map 4)

Dione glycera (C. & R. Felder 1861), as *Agraulis glycera* Wein. Ent. Monatschr., 5:102-103.

= *Dione moneta* forma *gnophota* Stichel 1907, Gen. Ins., fasc. 63, p. 30, pl. 1, fig. 4.

This orange and black butterfly (Seitz, 1913, pl. 84f) occurs in South America from western Venezuela along the eastern slopes of the Andes through Ecuador, Peru and Bolivia to northern Argentina (Hayward, 1952). This is an upland species and rarely descends below 1,000 metres (Hall, 1921) and there has been no differentiation into subspecies. The sexes are similar. Presumably due to the transposition of the plates in Seitz (1913) with those of *D. moneta*, a considerable quantity of museum material has been incorrectly identified and naturalists' field notes are difficult to assign to the correct species. The map indicates the gross range within which *glycera* has been found; it does not necessarily occur everywhere within it, for museum data are scanty.

Podotricha Michener

Podotricha Michener 1942, Amer. Mus. Novit. No. 1197, p. 3, figs. 2, 11.

Genotype: *Colaenis euchroia* Doubleday 1847, = *Colaenis* Hübner 1819 (Part), Verz. bekannt. Schmett., p. 32.

The distribution of the species of this genus is handicapped by the paucity of authentic localities, for many data labels only reveal the headquarters of collectors and not the sites of capture. Suspect localities are indicated as such on the maps, which contain all the indentifiable localities of specimens in the museums visited, together with information communicated by Cornell University.

Both species seem local and solitary. The food plants and immature stages are unknown. They are upland butterflies, but they do not reach the higher peaks and are probably limited to between 1,200 and 2,400 metres. Of the approximately 150 specimens examined, less than 5% were females. There is no sexual dichromatism, so presumably the habits of the females prevent them from coinciding with the paths of collectors. The terrain inhabited by these species is rugged and precipitous, so the sites of the food plants may be quite inaccessible to the general

collector, though the males would be taken feeding on flowers after the females had retired to seek sites for oviposition.

Podotricha euchroia (Doubleday)

(Text-figs. 8, 48, 65, 86, 112, 130, 141, 143, 153; Map 6)

Podotricha euchroia (Doubleday 1847), as *Colaenis euchroia*, Gen. Diurn. Lep. p. 149, pl. 20, fig. 3.

This butterfly (Seitz, 1913, pl. 84c), which has a yellow or orange ground color with black markings, occurs in South America on the Andean highlands from just inside the Venezuelan border in the Cord de Merida, through Colombia and Ecuador to Peru at lat. 5° South. The locality "Cuzco" on two specimens in the Paris Museum is suspect, for it is 800 miles south of the nearest other record. A specimen in the Hope collection labelled "Para" is almost certainly in error. The sexes are alike.

Subspecies (1) *Podotricha euchroia euchroia* (Doubleday 1847) (*loc. cit.*).

This subspecies has a deep orange ground color and occurs only in the northern half of the range of the species. In the Cauca Valley the ground color may be more yellow and was described as *caucana* by Riley (1926, Entomologist, 59: 242), though it seems to occur sympatrically with the typical form and may be a seasonal variety.

Subspecies (2) *Podotricha euchroia mellosa* (Stichel 1906), as *Colaenis euchroia mellosa*, Ins. Börse, 23:208.

This subspecies occupies the southern half of the range and has a straw-colored ground color with more extensive dark markings than the typical form. The transverse light yellow bar on the hindwing is white at the base, though this is variable and may be white along almost its whole length, a form to which the name *straminea* was given by Riley (1926, *ibid.*). As *mellosa* and *straminea* do not seem to be geographically or ecologically isolated, it is possible they also are seasonal forms.

The only geographical feature separating the distribution of the subspecies *euchroia* and *mellosa* is the valley of the Rio Patia, which does in fact separate them exactly. It is unfortunate that not only are there few museum specimens available for study, but of those there are even fewer which have precise locality data. Field observations suggest that this is a species preferring altitudes in the range 1,000-2,000 metres and such records as Guayaquil are probably ports of embarkation and not sites of collection.

Podotricha telesiphe (Hewitson)

(Text-figs. 7, 26, 47, 66, 113, 131, 153; Map 7)

Podotricha telesiphe (Hewitson 1867), as *Colaenis telesiphe*, Trans. Ent. Soc. Lond. (Ser. 3), 5:564.

This dark brown butterfly (Seitz, 1913, pl. 84d) with orange markings on the forewings occurs on the eastern slopes of the Andean highlands from northern Ecuador to Bolivia at 17° South. The sexes are similar. Two forms may be distinguished by the color of the transverse band on the upper surface of the hindwing.

Subspecies (1) *Podotricha telesiphe telesiphe* (Hewitson 1867) (*loc. cit.*).

This subspecies, which has a white transverse band on the hindwing, occupies the southern part of the range from about lat. 2° South to 18° South. It is uniform over its range and occurs sympatrically with *Heliconius telesiphe telesiphe* Doubleday 1847 (Map 8), which is very similar in appearance.

Subspecies (2) *Podotricha telesiphe titraustes* (Salvin 1871), as *Colaenis titraustes*, Ann. Mag. Nat. Hist. (Ser. 4), 7:415.

This form may be distinguished from *P. t. telesiphe* by the bar on the hindwing, which is yellow instead of white. It occurs between lat. 1° North and 2° South, a range it shares with *Heliconius telesiphe sotericus* Salvin 1871 (Map 8), which also has the bar of the hindwing yellow. Many museum specimens have the names of the two forms of *P. telesiphe* transposed, presumably because Seitz (1913) made this error and subsequent workers have overlooked the correction on pages 1134 and 1139 of his text. In the collection of the University of Central Ecuador in Quito there are some specimens of *P. telesiphe* from Puyo which have the transverse bar cream. These are the only known intermediates between the two color forms and Puyo is on the mutual boundary of their ranges. There is a specimen of *H. t. telesiphe* in the British Museum labelled "Bogotá" and a specimen of *H. t. sotericus* in the British Museum (Tring) labelled "British Guiana," both of which are certainly in error.

There are no biological data available on the distastefulness of either *P. telesiphe* or *H. telesiphe*, and though this probable example of intergeneric mimicry has been known for many years, a full understanding seems no nearer. The significant features are that these two genera are not very closely related, yet not only are these species generally similar in appearance but the two color forms of each have an identical distribution and, according to field reports, fly together. There are no conspicuous geographical features separating the two subspecies of *P. telesiphe* and *H. telesiphe* but east of the Gulf of Guayaquil the Andes are invaded by deeper east-west valleys than elsewhere, though the

minimum altitude is still within the normal range of the two species.

Dryas iulia (Fabricius)

(Text-figs. 1, 2, 6, 22, 25, 42, 43, 46, 67, 79, 85, 89, 95, 99, 114, 126, 144, 153; Map 9; Pl. I, Fig. 4)

Dryas Hübner 1807, Monobasic, figured in Samml. Exot. Schmett., 1, pl. 43, 4 figs.

Genotype: *Papilio iulia* Fabricius 1775, designated by Hemming, 1934, Entomologist, 67:156.

= *Colaenis* Hübner 1819, (Part), Verz. bekannt. Schmett., p. 32.

Genotype: *Papilio iulia* Fabricius 1775, designated by Scudder 1875, Proc. Amer. Arts Sci., 10:146.

Dryas iulia (Fabricius 1775), as *Papilio iulia*, Syst. Ent., p. 509.

This bright orange butterfly with black markings on the upper surface of the wings (Seitz, 1913, pl. 84b) occurs from Florida and eastern and western Mexico at lat. 30° North, through the Bahamas, the Greater and Lesser Antilles and Central America to South America. East of the Andes it extends to 35° South, and on the western slopes it has been recorded as far south as Loja (4° South). It is doubtful if it occurs much above 1,500 metres, though it occupies very varied habitats below this altitude. It is a common and conspicuous butterfly which is fairly easy to catch, both in flight and during its habit of resting in the sun on damp earth.

Throughout its range it has become differentiated into geographical subspecies which differ in their ground color, the intensity and extent of the black markings and in the distribution of the androconia on the forewing veins of males. The sexes can be distinguished by the presence of a second dark bar on the forewings of females and the generally more diffuse nature of the pattern.

Subspecies (1) *Dryas iulia iulia* (Fabricius 1775), as *Papilio iulia*, (*loc. cit.*).

The typical subspecies ranges from the eastern and western coasts of Mexico at lat. 30° North through Central America to South America where, on the eastern side of the Andes, it extends throughout the whole of the Amazon Basin and Brazilian savannas and is generally distributed as far as 35° South. It also occurs in Trinidad and Tobago. The ground color when fresh is a rich orange with intense dark markings on the upper surface of the wings, though specimens from Central America and Mexico are lighter in color and have less distinct markings. The androconia on the forewings of males are present only on veins Cula, Cu1b and 1A.

Subspecies (2) (?) *Dryas iulia moderata* (Stichel 1907), as *Colaenis iulia delila* forma *moderata*, Gen. Ins., fasc. 63, p. 12.

Originally described from a male from Honduras, this pale, and in males almost immaculate, form occurs in eastern and western Mexico through Central America to the western slopes of the Ecuadorian Andes at least as far south as Loja. Grossly, its range appears to overlap that of the typical form in Mexico and Central America, but in southwestern Colombia and western Ecuador it replaces it completely and is subject to a small amount of variation. The distribution of androconia is similar to that of typical *Julia*. Museum locality data cannot be treated quantitatively and are not always reliable, but the wide range of *moderata* and its apparent overlap with *Julia* suggests it is neither ecologically isolated nor is it the result of environmental effects on the larvae, though there is no experimental evidence to indicate whether *moderata* characters are heritable or not. The most plausible explanation is that the immaculate form is typical of the southwestern extremities of the range of the species and the genes or loss of genes responsible for the immaculate appearance have spread into the northwest where they form a proportion of a polymorphic population.

The similarity in appearance, habits and habitat between *Dryas julia* and *Heliconius aliphera* has been noticed for many years. Though the range of *H. aliphera* is more restricted in the north, elsewhere they almost invariably fly together. The association of *D. i. moderata* with an almost equally immaculate form of *H. aliphera*, which is known only from sympatric localities, has suggested a mimetic association but little is known about their relative palatabilities. *D. julia titio* (Stichel 1907) (as *Colaenis julia titio*, Gen. Ins., fasc. 63, p. 12) is an allegedly fiery red form from Youngas de la Paz, Bolivia, which occurs sympatrically with the typical form and from which it cannot be separated on the museum specimens (Riley 1926).

Subspecies (3) *Dryas julia cillene* (Cramer 1779), as *Papilio cillene*, Pap. Exot., 3:38, pl. 215, figs. D and E.

This subspecies from Florida and the neighboring Keys is more pale than the typical form and has the dark markings reduced. The androconia of males are prominent on forewing veins Cu1a, Cu1b, and 1A but on some specimens from the Keys there are small numbers on one or more of the veins M1, M2 and M3.

The locality data of Cramer's original specimen ("Dutch Guiana") is certainly in error, for his figures, which are without description, are similar to the Cuban forms, but variation within the populations on neighboring islands could include this type. Had Cramer figured the males more accurately and included the black andro-

conia on the forewing veins, then these would have assisted in deducing the exact locality of his specimens. It is not known whether the type is still in existence or not, so Stichel's allocation of the name *nudeola* to the Cuban form must stand until reference to the type can prove Cramer's original specimen was also Cuban.

Subspecies (4) *Dryas julia nudeola* (Stichel 1907), as *Colaenis julia cillene* forma *nudeola*, Gen. Ins., fasc. 63, p. 12.

This subspecies from Cuba, the Isle of Pines and Grand Cayman is similar to *cillene* but in males the forewing bar is represented by a pair of dark spots which are, or are just not, in contact. In the dozen specimens examined from eastern Cuba the forewing androconia are abundant on veins M1, M2, M3, Cu1a, Cu1b and 1A.

Subspecies (5) *Dryas julia carteri* (Riley 1926), as *Colaenis julia carteri*, Entomologist, 59:240, pl. 2, fig. 1 [B.M. RH. 9223 and 4, Nassau].

This subspecies from the Bahamas Islands is similar to *cillene* in color and in the extent of the dark markings of the forewings, which in males are clearly separate. Androconia are present on forewing veins M1, M2, M3, Cu1a, Cu1b and 1A, a feature shared with *nudeola*, but some specimens from the western islands show only traces of androconia on the median veins, in which respect they grade into *cillene* from Florida. It has been taken from Nassau, Long Island, Cat Island, Eleuthera Island, Berry Island and New Providence (Rindge, 1955).

Subspecies (6) *Dryas julia delila* (Fabricius 1775), Syst. Ent., p. 510. First figured by Sloane, 1725, Nat. Hist. Jam. II, p. 215, pl. 239, figs. 21, 22, as *Papilio major*.

The males of this exclusively Jamaican subspecies are entirely immaculate above and are similar to extreme examples of *moderata*, but can be distinguished by the lighter and broader wings which lack the narrow black margin, and by the very heavy investment of androconia on forewing veins M1, M2, M3, as well as on Cu1a, Cu1b and 1A.

Subspecies (7) *Dryas julia hispaniola* (Hall 1925), as *Colaenis julia hispaniola*, Entomologist, 53: 186.

This subspecies from Hispaniola is similar to *nudeola* but has a slightly greater development of the dark markings, so that in males the forewing spots are fully confluent, making an incomplete bar. From the small number of specimens available, it seems there is variation in the distribution of androconia, for some have them strongly developed on six forewing veins whereas the others have the three more anterior veins only sparsely invested.

Subspecies (8) *Dryas iulia juncta* Comstock 1944, *Sci. Surv. Puerto Rico*, 12:441, figs.

This subspecies from Puerto Rico and St. John is similar to *hispaniola* except that the dark markings are more fully developed and the forewing is traversed by a complete, through irregular, bar. The androconia of the forewing seem to be confined to the posterior three veins, though this observation is based on an examination of only three specimens.

Subspecies (9) *Dryas iulia warneri* (Hall 1936), as *Colaenis iulia warneri*, *Entomologist*, 69:276. [B.M. 1936-736, St. Kitts].

This form from St. Kitts has not been examined.

Subspecies (10) *Dryas iulia dominicana* (Hall 1917), as *Colaenis iulia* var. *dominicana*, *Entomologist*, 50:161.

This subspecies from Dominica and Guadeloupe has a ground color similar to that of the Greater Antillean forms but has the bar of the forewing complete and forewing is deeper than in any of the other subspecies. The forewing androconia are well developed on M1, M2, M3, Cu1a, Cu1b and 1A.

Subspecies (11) *Dryas iulia lucia* (Riley 1926), as *Colaenis iulia lucia*, *Entomologist* 59:241, pl. 2, fig. 4. [B.M. RH. 10115, St. Lucia].

This subspecies from St. Lucia and Martinique has a rich red ground color similar to that of the southern mainland forms, but with reduced dark markings so the forewing bar is represented only by two distinct small spots. It appears to differ also from *dominicana* in the absence of androconia on the median veins of the forewing, though this observation is based on an examination of only three specimens.

Subspecies (12) *Dryas iulia framptoni* (Riley 1926), as *Colaenis iulia framptoni*, *Entomologist*, 59:241, pl. 2, fig. 5, [B.M. RH. 10116-7, St. Vincent].

This last subspecies from St. Vincent, Barbados (where it is probably a migrant), Grenada and the Grenadine Islands has the upper side ground color, dark markings and distribution of androconia similar to the mainland *iulia*, but the underside is a more dark purplish brown.

Subspeciation in the area around Cuba, Florida, the Bahamas Islands and Hispaniola is in a very incipient state and a long series of specimens from each locality would be necessary to distinguish them with certainty. Though males from all localities have androconia on the two most anterior veins of the hindwing, there seems to be a center in this area of forms which have androconia on six forewing veins too, a feature found elsewhere only in specimens from Guadeloupe and Dominica. Outside these localities fore-

wing androconia occur only on the three posterior veins of the forewing (Cu1a, Cu1b and 1A), though in marginal areas like Florida Keys, eastern Bahamas and Hispaniola they may occur sparsely on the three more anterior veins (M1, M2 and M3). The explanation of the occurrence of the androconia on six forewing veins in Dominica and Guadeloupe is handicapped by a shortage of specimens, but if the absence of known intermediates on the neighboring islands is valid it suggests that the populations are more isolated on the eastern Caribbean Islands than elsewhere, a suggestion that is corroborated by the higher degree of subspeciation in that region. The contrast in the appearance of specimens from the eastern and western slopes of the Andes demonstrates that the mountains form a barrier that can only be circumvented round the spurs of northern Colombia. Elsewhere the lowest pass that could offer an east-west corridor is 2,500 meters high, that is, nearly 1,000 meters above the highest altitude *Dryas* is normally known to inhabit.

Heliconius Kluk

Heliconius Kluk 1802, *Zwierz. Hist. nat. pocz. gospod.*, 4:82.

Genotype: *Papilio charitonia* Linnaeus 1767. Designated by Hemming, 1933, *Entomologist*, 66:223.

The only species of *Heliconius* included in this paper are those that occur in Trinidad, and as the genus is to be the subject of a later publication the detailed distribution of subspecies and other forms will be deferred and no nomenclatorial or taxonomic changes will be suggested.

Heliconius aliphera (Godart 1819)

(Text-figs. 20, 41, 57, 77, 122, 133, 134, 147, 153; Map 10; Pl. I, Fig. 7)

This orange and black butterfly (Seitz, 1913, pl. 80a) is very similar to a small *Dryas*, with which it flies over almost all of its range. The variations in the intensity and extent of the black markings parallel those of *Dryas*, with which they occur sympatrically. In Central America there are a number of closely allied forms which may or may not be conspecific.

Heliconius isabella (Cramer 1781)

(Text-figs. 19, 40, 56, 78, 92, 101, 123, 135, 146, 153; Map 11; Pl. I, Fig. 6)

Though fairly constant in Trinidad, this black and orange butterfly (Seitz, 1913, pl. 80d) is variable elsewhere and without a more detailed study it is difficult to define its limits with accuracy. Its habitat includes both forest and forest margins, so the absence of records from the llanos of Venezuela and the savannas of eastern Brazil is probably real.

Heliconius numata (Cramer 1780)

(Text-figs. 15, 27, 49, 71, 90, 116, 136, 153; Map 12; Pl. I, Fig. 9)

This yellow and/or orange and black butterfly (Seitz, 1913, pl. 72), which is frequently considered to be a Müllerian mimic of members of the Danaidae and Ithomiidae, occurs in Trinidad in two polymorphic forms, one with a predominantly orange ground color, and one with a greater proportion of yellow, which is particularly noticeable on the hindwing. On the mainland the diversity of *numata*, or its very close relatives, is extremely great, so pending a revision of the genus the distribution map can only include those forms which are similar to those of Trinidad. It seems likely that further study will show that many of the named varieties and geographical forms will subsequently be shown to be conspecific with *numata*, and its range will include the western slopes of the Andes and more southerly regions of eastern South America.

Heliconius doris (Linnaeus 1764)

(Text-figs. 13, 29, 52, 72, 117, 139, 153; Map 13; Pl. I, Fig. 14)

This black and yellow butterfly (Seitz, 1913, pl. 77c) is known to be polymorphic, both in Trinidad and elsewhere, and commonly exhibits blue, red or green on the hindwing. It is a forest butterfly and unlikely to occur in the savanna areas.

Heliconius wallacei Reakirt 1862

(Text-figs. 12, 28, 50, 70, 91, 115, 138, 153; Map 14; Pl. I, Fig. 13)

This blue, black and yellow forest butterfly (Seitz, 1913, pl. 77e) is relatively constant over its whole range, which is similar to that of *H. sara*, with which it frequently flies. There is a similarity also in that in some localities there is a delicate white margin to the posterior border of the hindwings. Specimens are known from diverse localities within the range of the species in which the yellow markings are replaced by white.

Heliconius melpomene (Linnaeus 1702).

(Text-figs. 14, 30, 51, 73, 100, 118, 137, 153; Map 15; Pl. I, Fig. 8)

In Trinidad this butterfly is monomorphic and is black with a broad red patch just distal to the center of each forewing (Seitz, 1913, pl. 76b). In the Amazon Basin it is highly polymorphic and its pattern may include a red base to the forewing and red radiating lines on the hindwing. There is also great diversity in the expression of the red patch, which may be entire or broken into spots, broad or narrow, red or yellow or a

combination of the two (Seitz, 1913, pls. 75, 76). Towards the extremities of its mainland range the degree of polymorphism declines and geographical localities have characteristic forms. It is impossible to treat museum data quantitatively, so without personal experience of each locality it is not possible to state reliably which are dominant morphs, but museum material probably indicates the number of patterns that are present. On the western slopes of the Andes the form known as *H. cythera* is conspecific with *melpomene* and grades round the tips of the Andean spurs in Colombia through such types as *modesta* and *vulcanus*. *H. xenoclea* is also conspecific with *melpomene*. The breeding experiments upon which these statements are based will be the subject of a later paper.

Heliconius erato (Linnaeus 1758)

(Text-figs. 16, 21, 31, 53, 74, 80, 103, 119, 140, 152, 153; Map 15; Pl. I, Fig. 10)

The remarkable relationship between *H. melpomene* and *H. erato* has aroused the interest of biologists for many years and is currently a principal topic of investigation by workers both in the Americas and in Europe. The two species, though systematically and biologically quite distinct, show a similarity to each other both in color and pattern which follows their profound geographical and polymorphic variation (Seitz, 1913, pl. 78). Grossly their range appears to be identical, and they frequently fly together, though *melpomene* tends to prefer the interior of the forest and *erato* the margins. The very diverse appearance of some of the forms, as with *melpomene*, led earlier taxonomists to erect many more species than should in fact be the case and there is now no doubt that forms like *cyrbia*, *venus* and *microclea* are all conspecific with *erato*. The breeding evidence for this will be published later.

Heliconius sara (Fabricius 1793)

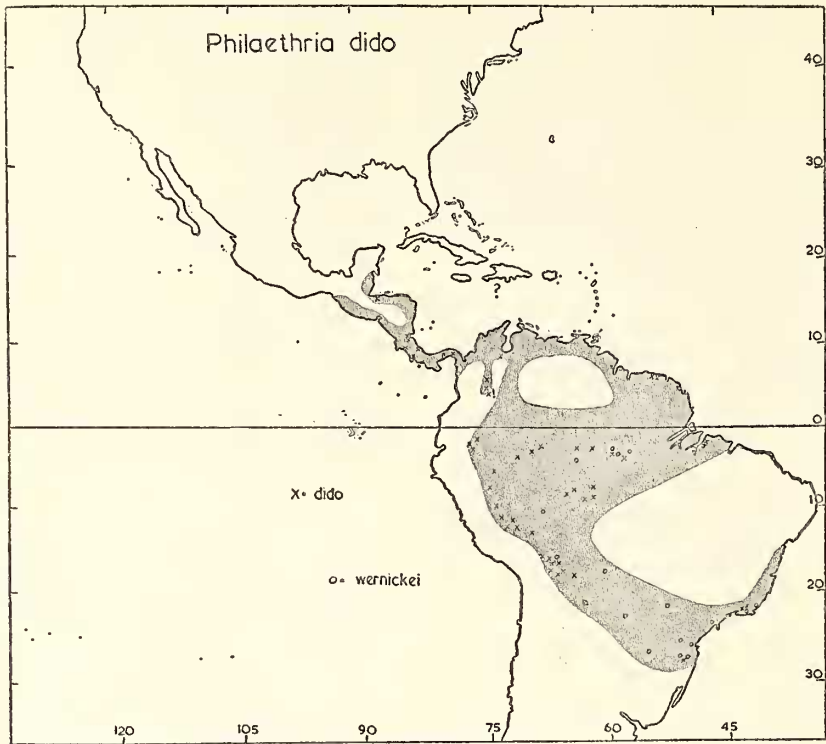
(Text-figs. 18, 32, 54, 75, 102, 120, 153; Map 16; Pl. I, Fig. 12)

This black, blue and yellow butterfly (Seitz, 1913, pl. 77f) is fairly constant over its range though some specimens, which in some localities form the predominant or only form, have the posterior margins of the hindwings white. It is a forest butterfly so the lack of records from the llanos of Venezuela and the savannas of eastern Brazil may be correct.

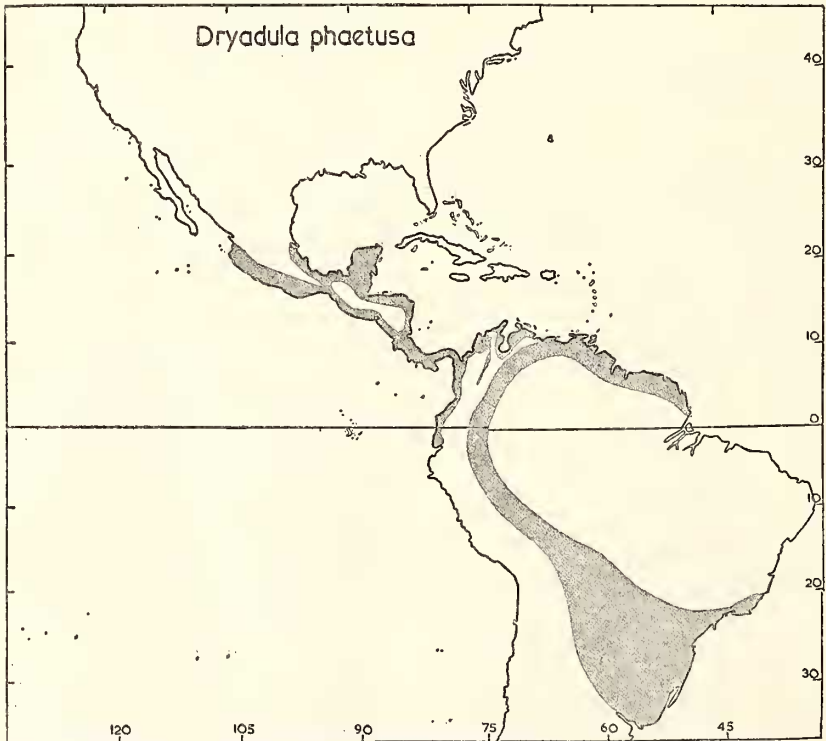
Heliconius ricini (Linnaeus 1705)

(Text-figs. 17, 33, 55, 76, 121, 153; Map 17; Pl. I, Fig. 11)

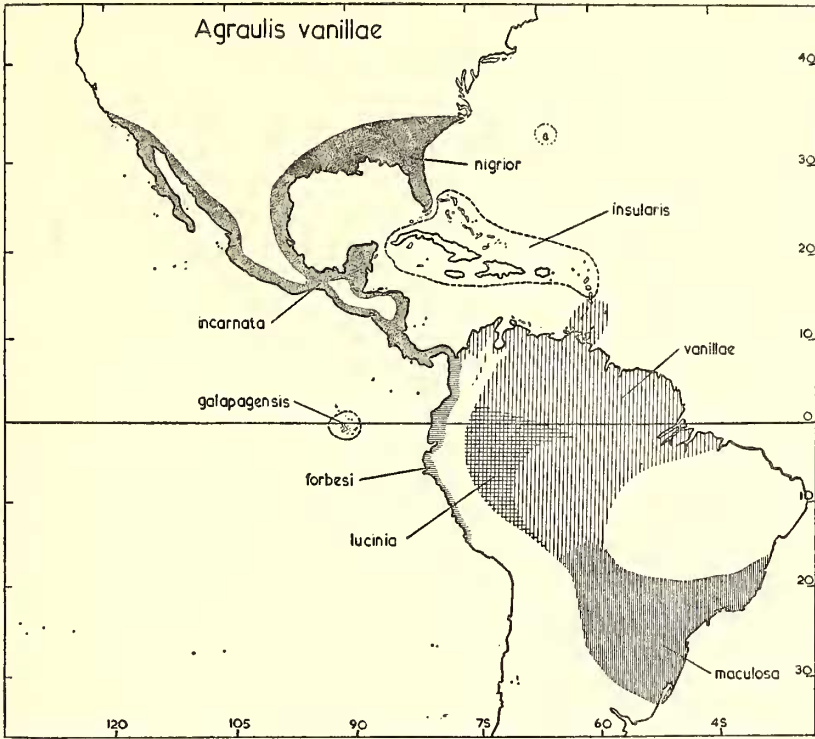
This black, yellow and red butterfly (Seitz, 1913, pl. 79d) is very constant over its range, and is apparently restricted broadly to the coastal strip of northeastern South America.



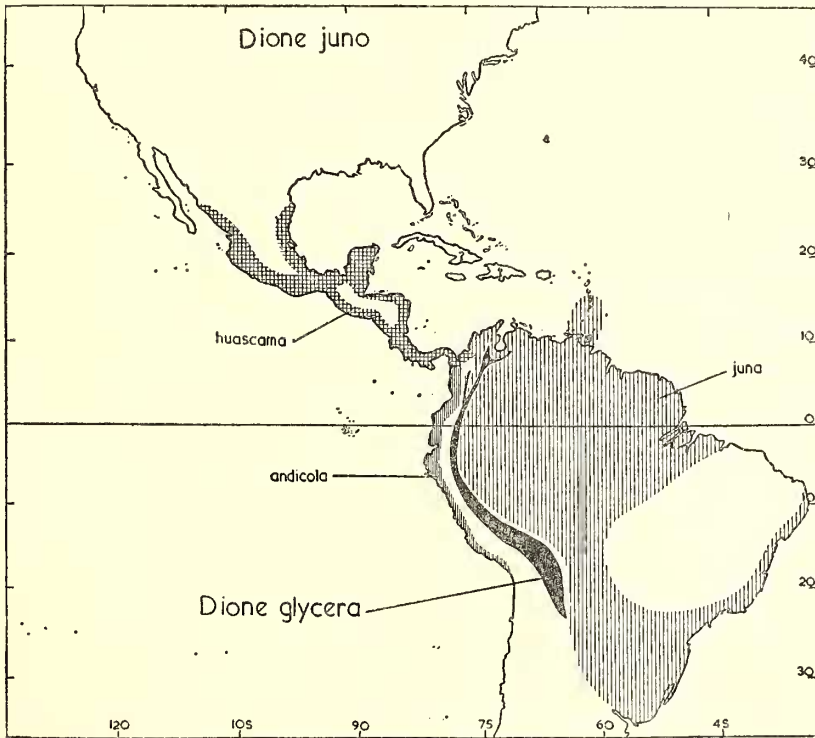
Map 1. *Philaethria dido*.



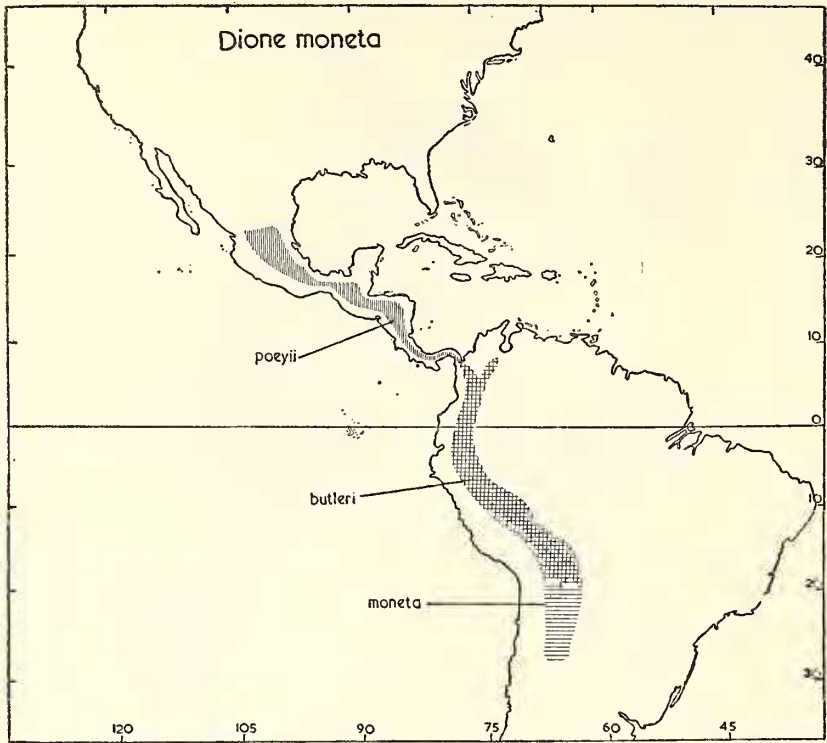
Map 2. *Dryadula phaetusa*.



Map 3. *Agraulis vanillae*.



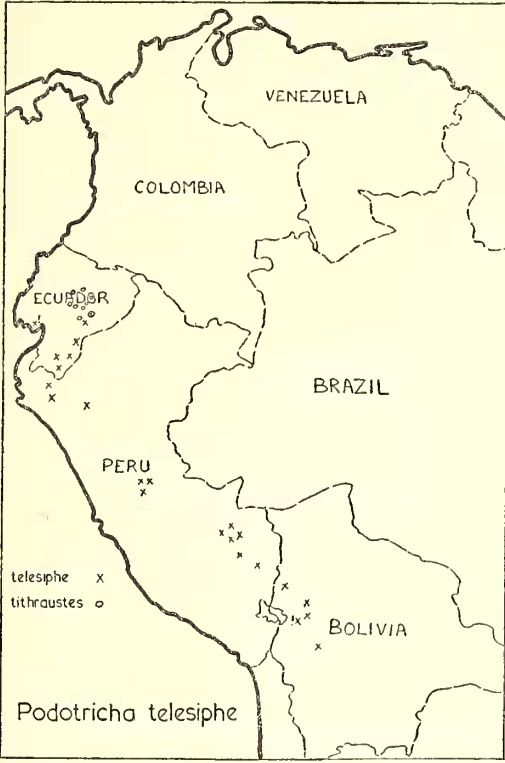
Map 4. *Dione juno* and *Dione glycera*.



Map 5. *Dione moneta*.



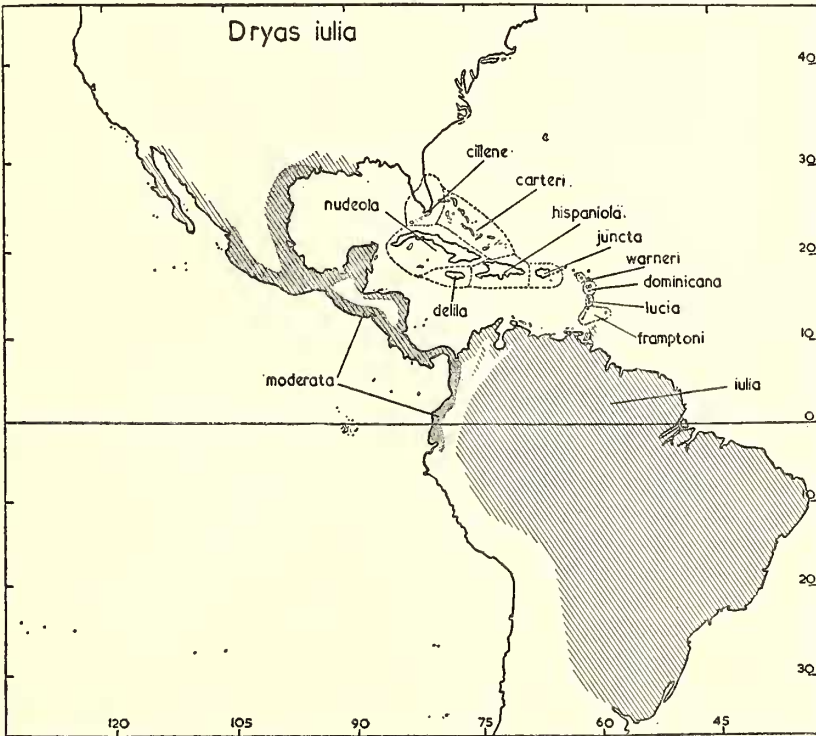
Map 6. *Podotricha euchroia*.



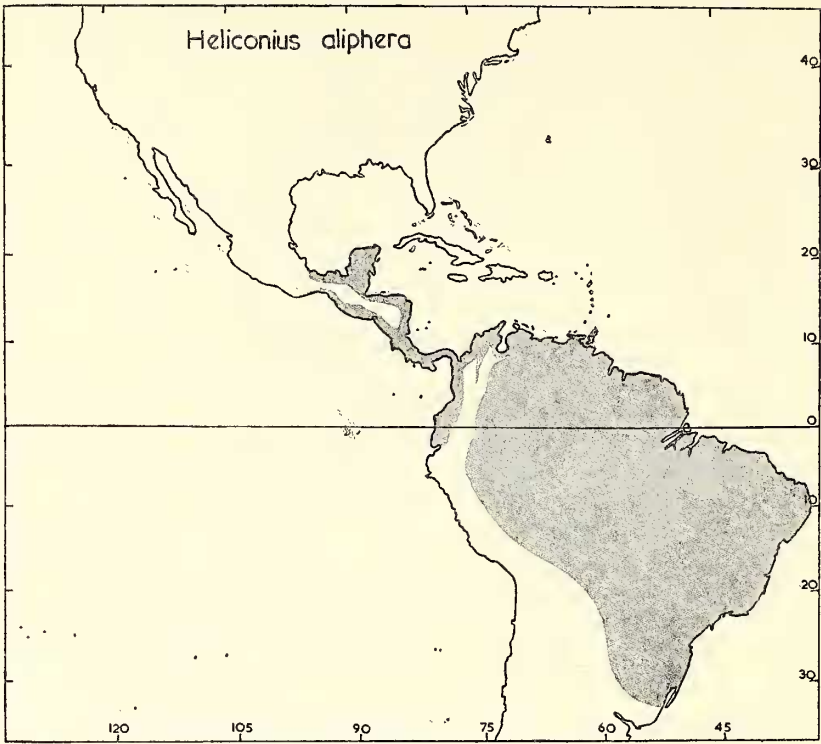
Map 7. *Podotricha telesphe*.



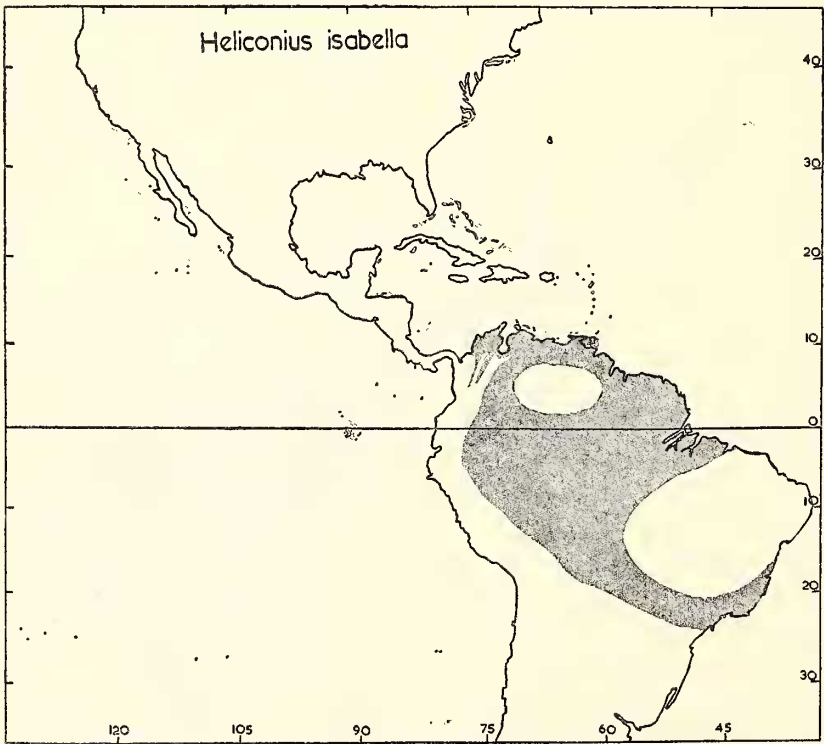
Map 8. *Heliconius telesphe*.



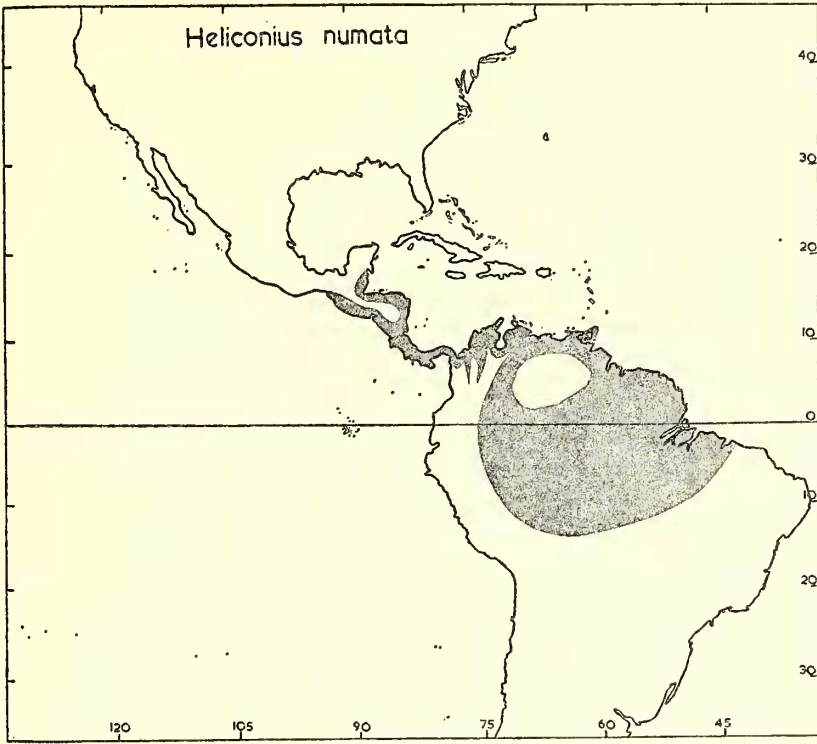
Map 9. *Dryas iulia*.



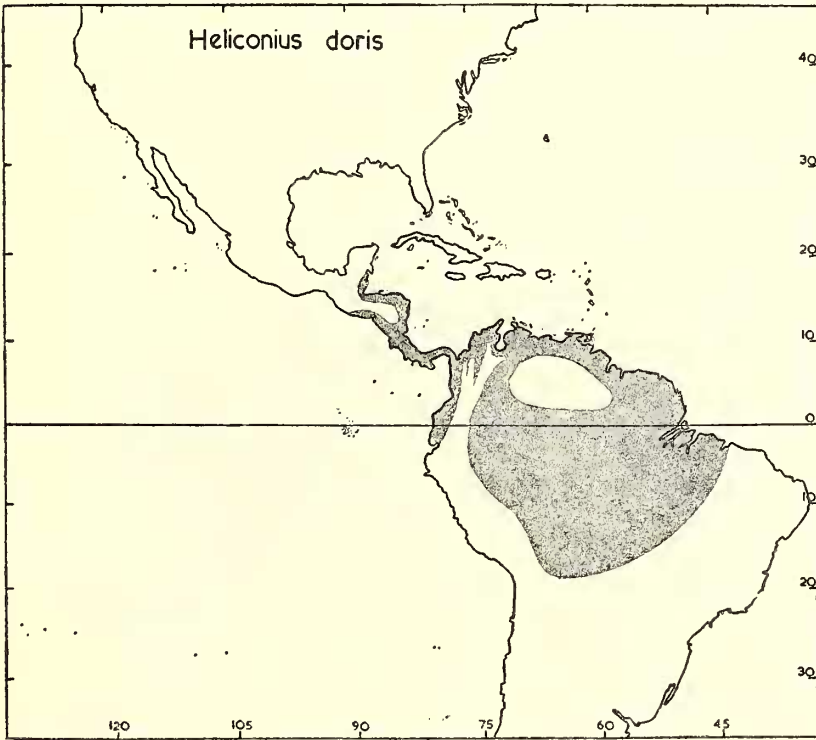
Map 10. *Heliconius aliphera*.



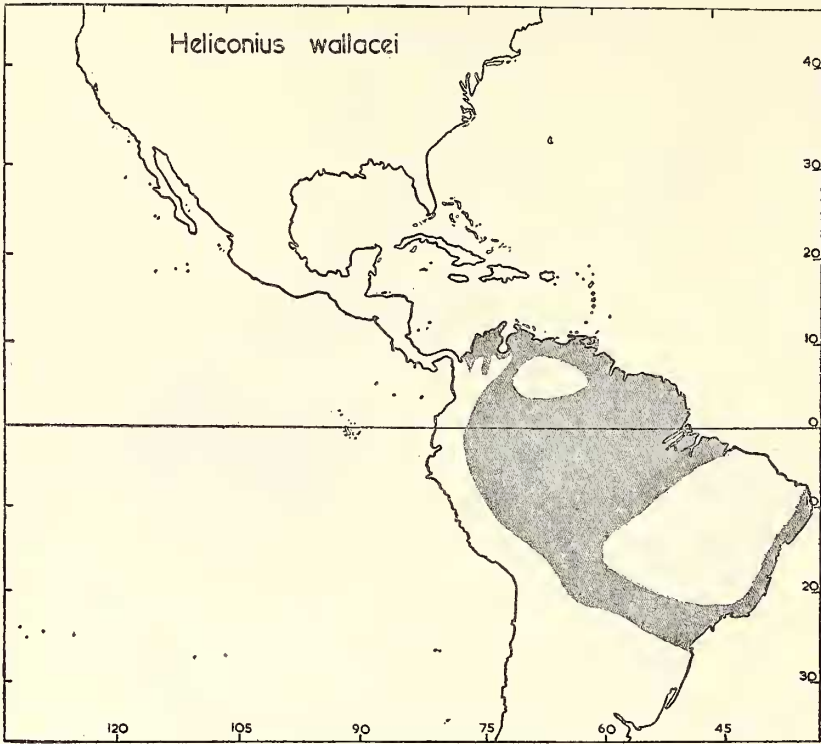
Map 11. *Heliconius isabella*.



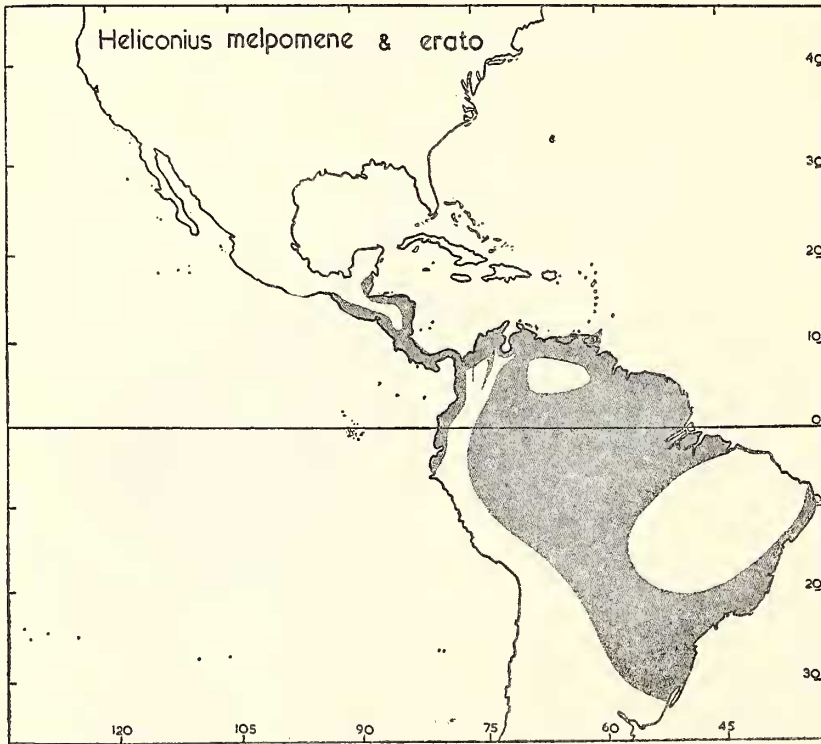
Map 12. *Heliconius numata*.



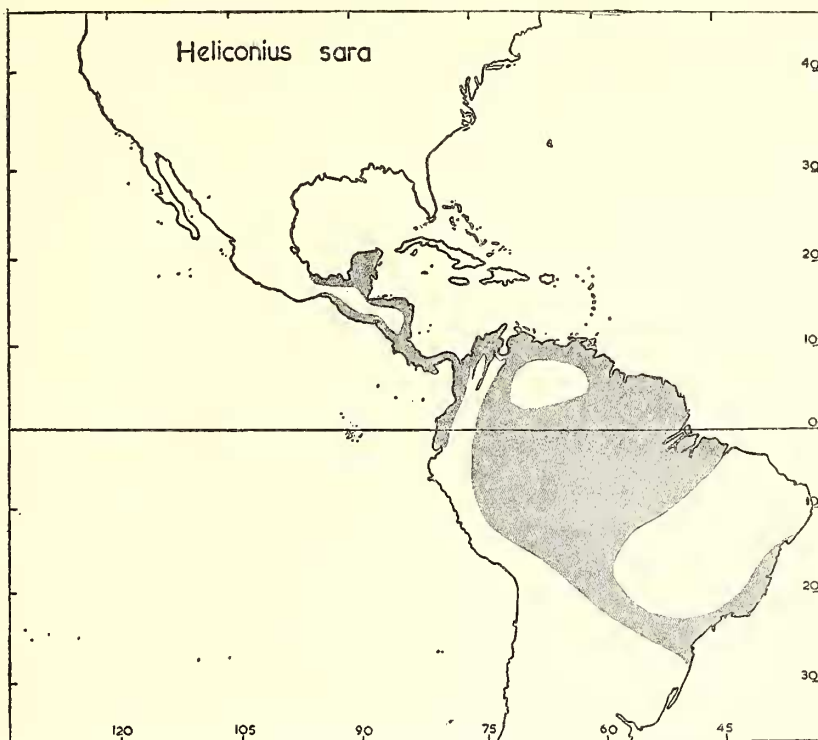
Map 13. *Heliconius doris*.



Map 14. *Heliconius wallacei*.



Map 15. *Heliconius melpomene* and *erato*.



Map 16. *Heliconius sara*.



Map 17. *Heliconius ricini*.

III. FIELD KEY TO THE ADULTS OF TRINIDADIAN HELICONIINAE

- | | | |
|---|--------------------------|----|
| 1. Humeral vein of hindwing recurrent and unbranched (Key-fig. A ¹) | HELICONIINAE | 2 |
| Humeral vein of hindwing otherwise | OTHER GROUPS | |
| 2. Discal cell of hindwing open (Key-fig. A ²) | | 3 |
| Discal cell of hindwing closed (Key-fig. B ¹) | <i>Heliconius</i> | 7 |
| 3. Green ground color with black markings | <i>Philaethria dido</i> | |
| Orange ground color with black markings | | 4 |
| 4. Underside with pearly-silver spots | | 5 |
| Underside without pearly-silver spots | | 6 |
| 5. Androconia of males absent on hindwing veins; distal margin of forewings smooth; dark band on posterior border of hindwing spotted with ground color | <i>Agraulis vanillae</i> | |
| Androconia of males present on five veins of the hindwing (M1, M2, M3, Cula & Culb) (Key-fig. C); distal margins of forewings scalloped; dark band on posterior border of hindwing complete, unspotted | <i>Dione juno</i> | |
| 6. Androconia of males absent on hindwing; upper and lower surface of hindwing traversed by median dark bar; wings broad | <i>Dryadula phaetusa</i> | |
| Androconia of males present on two anterior veins of hindwing, (Sc + R1 and Rs), (Key-fig. D); hindwing with dark border only, wings narrow | <i>Dryas iulia</i> | |
| 7. Ground color predominantly black | | 8 |
| Ground color predominantly orange or orange and yellow | | 13 |
| 8. Forewing with single red patch | | 9 |
| Forewing with two yellow patches or bars | | 10 |
| 9. Base of underside of hindwing with 3 red spots (Key-fig. E) | <i>H. melpomene</i> | |
| Base of underside of hindwing with 4 red spots (Key-fig. F) | <i>H. erato</i> | |
| 10. Base of upper side of forewing with blue sheen | | 11 |
| Base of upper side of forewing without blue sheen | | 12 |
| 11. On the underside of the hindwing a semicircular red streak interrupted by the bases of the hindwing veins, not extending towards the centre of the wing (Key-fig. G) | <i>H. wallacei</i> | |
| On the underside of the hindwing a semicircle of red spots, which curve towards the centre of the wing (Key-fig. H) | <i>H. sara</i> | |
| 12. Anterior half of hindwing red, with a boundary parallel with posterior margin | <i>H. ricini</i> | |
| Base of hindwing red, blue or green breaking up postero-distally into radiating streaks | <i>H. doris</i> | |
| 13. Dorsal ground color orange; wings dorsally edged with black, forewings crossed with two narrow black bars only. Similar to <i>Dryas</i> in appearance but smaller, wing span less than 6 cm when spread | <i>H. aliphera</i> | |
| Dorsal ground color orange and yellow with black spots, some coalesced; dorsal and ventral pattern similar | | 14 |
| 14. Underside of forewing with a pair of discrete round dark spots about the middle of the wing; the three anterior white spots on the distal margin of the underside of the hindwing approximately equal in size; and which if expressed on the dorsal surface are not yellow | <i>H. isabella</i> | |
| Underside of forewing, though with dark markings, without a conspicuous pair of round dark spots; the two anterior white spots on the anterior margin of the underside of the hindwing conspicuously larger than the succeeding ones and one or more are expressed on the dorsal surface as a yellow spot | <i>H. numata</i> | |

In Trinidad the vernacular names for the Heliconiinae are: Silver Spotted Flambeau—*Dione juno* and *Agraulis vanillae*; Flambeau—*Dryas iulia*; Caroni Flambeau—*Dryadula pha-*

tusa; Small Flambeau—*Heliconius aliphera*; Grecian—*H. wallacei*, *H. doris*, *H. sara* and *H. ricini*; Postman—*H. erato* and *H. melpomene*; Tiger—*H. isabella* and *H. numata*.

IV. MORPHOLOGY

METHODS OF MORPHOLOGICAL STUDY

Unless otherwise stated, the drawings and conclusions are the result of the study of at least fifteen examples of each structure, from individuals taken from diverse geographical localities. All the locally available material was killed, examined, and drawn in alcohol, but in the case of some of the exotic species reliance had to be placed on dry pinned museum specimens. Semi-permanent preparations were mounted in polyvinyl alcohol and permanent preparations in clear mount or CMC. Where necessary, material was macerated in potassium hydroxide prior to detailed examination, for which a binocular dissecting microscope with magnifications up to $\times 100$ and a spot lamp was found satisfactory for all but the smallest structures. A monocular with oil immersion objectives was used for minute structures, such as androconia. For accuracy of proportion the drawings were made with an eye-piece grid and squared paper. Pupal tracheation was obtained from living material, three-quarters through development, dissected under glycerine. De-scaling was found to be most easy in water to which detergent had been added. The examination of the copulatory mechanism was accomplished by the killing of copulating pairs with the electrocuting technique described by Emsley (1958).

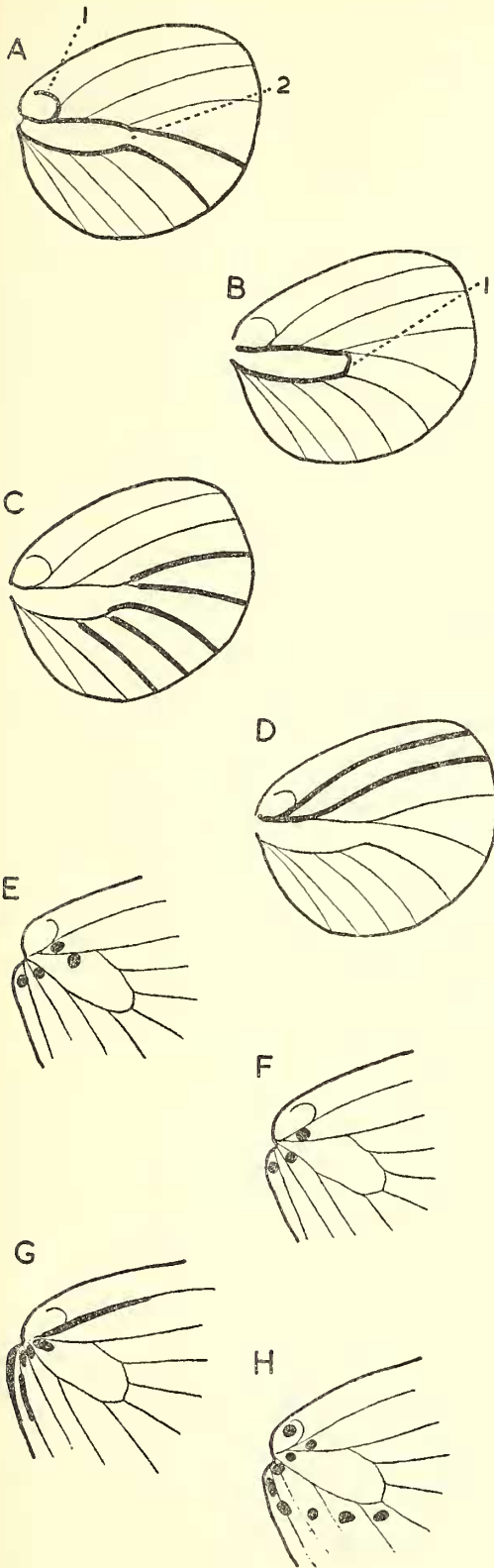
The object of a paper of this kind is the discovery of features common to distinct species which will unite them at higher level, not their separation into smaller groups, hence biometry has little pertinence. In principle, qualitative rather than quantitative characters have been sought.

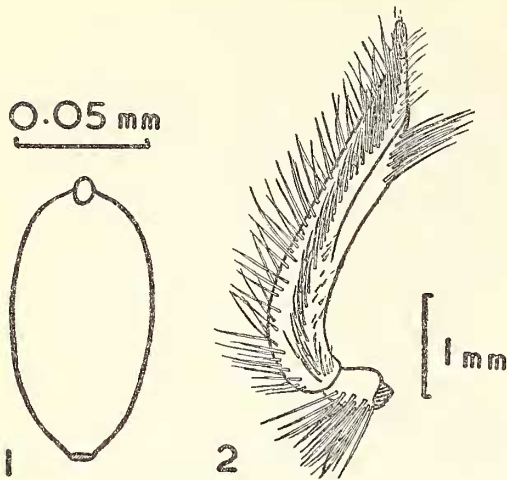
EXTERNAL ANATOMY

HEAD (Text-figs. 1-20)

Head Capsule: The head capsule of *Dryas*, when compared with the heads of other genera, revealed no structures of taxonomic value. From the drawings by Ehrlich & Ehrlich (1962) it appears that the head capsule musculature characters are similar in *Dryas iulia* and *Heliconius charitonius*, and these two differ from *Agraulis vanillae* only in the degree of development of two muscles. Though these are the only members of the Heliconiinae discussed in that paper, no other described members of the Nymphalidae are as similar.

Mouthparts: In all the species studied, each galea has a row of erect ovoid tubercles on the anterior surface of the distal fifteenth of its length. Each tubercle has a small terminal papilla (Text-fig. 1). Taylor (1957) showed that the





TEXT-FIG. 1. Papillate tubercle of proboscis of *Dryas iulia*.

TEXT-FIG. 2. Left view of left maxillary palp of *Dryas iulia*.

proboscis of Lepidoptera has little systematic value below family level, a view supported here, for no differences could be detected either between or within genera. The palps are held erect, closely applied to the sides of the base of the proboscis, but the statement by Doubleday & Westwood (1846) that their origins are widely separate cannot be confirmed.

In both sexes of all genera the palps are three-jointed and densely clothed posteriorly and laterally with elongate scales and anteriorly with erect hairs. Though no special structures of systematic value were observed, the degree of hairiness is least in *Philaethria*, *Dryadula* and *Dryas* (Text-fig. 2) and increases in density through *Heliconius*, *Agraulis* and *Dione* to *Podotricha*.

Antennae: (Text-figs. 3-20). The antennae of all species differ either in the shape of the club or in relative length, but no special structures were noticed and neither the distribution of the investment of the scales nor the shape appear to have much taxonomic value. This general conclusion was reached by Bodine (1896) and supported by Michener (1942a). *Philaethria* (4), *Agraulis* (5), *Dione* (9, 10, 11) and *Podotricha* (7, 8) have a greater development of the club than *Dryas* (6), *Dryadula* (3) and *Heliconius* (12-20).

THORAX

An examination of the thorax and axillary wing sclerites revealed no differences of value either within or among genera.

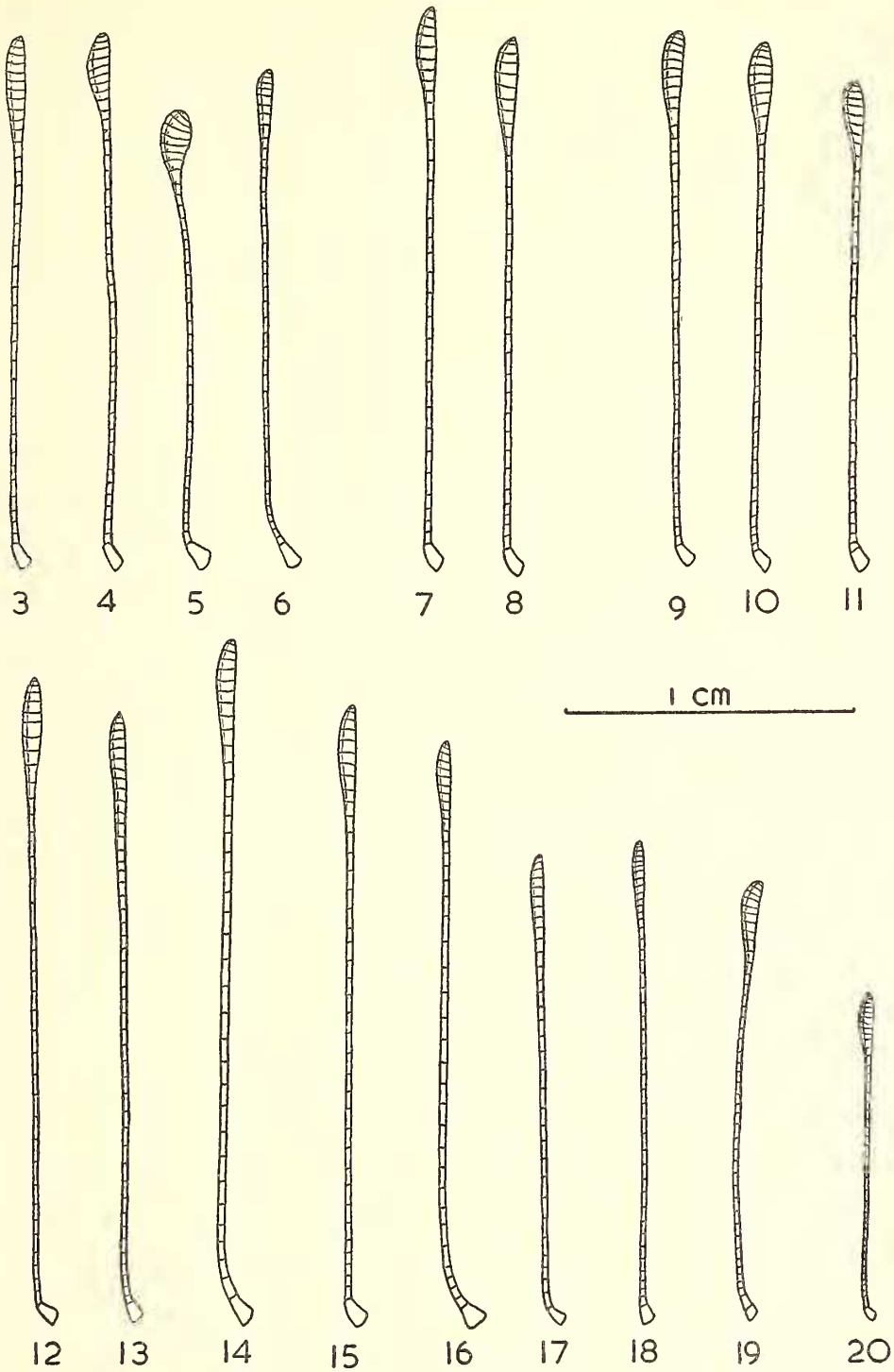
The prothoracic legs (Text-figs. 21-41) are sexually dimorphic. In males the tarsus consists of only one sclerite, bears no evidence of a pre-

tarsus, and is fused immovably to the tibia (Text-fig. 21). As noticed by Godman & Salvin (1901), the proportionate lengths of the leg segments of some species are specifically characteristic, though these do not aid the understanding of specific relationships.

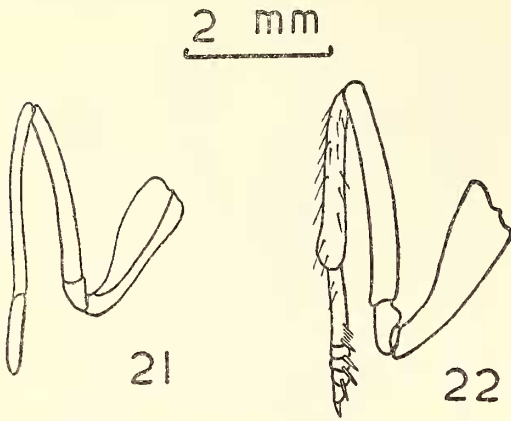
In females the reduction of the forelegs is principally due to compaction of the tarsi (Text-fig. 22), which are severely limited in their movement and are normally held closely applied to the ventral surface of the meso-thorax. Comparison of the foretarsi shows that the least modified and presumably the most primitive are *Philaethria* (23), *Dryadula* (24), *Dryas* (25), *Podotricha* (26), *Heliconius numata* (27), *H. wallacei* (28), *H. doris* (29), *H. melpomene* (30), *H. erato* (31) and *H. sara* (32), which are all basically similar, with the proximal tarsal segment of nearly normal length and with tarsal segments 2, 3, 4 and 5 reduced almost to annuli. The most distal segment bears a terminal spine which presumably represents the degenerate pretarsus. Within *Dione*, *D. juno* (34, 35) has the terminal spine reduced to a prominence, *D. glycera* (36) has the prominence finer and set in a shallow vertical groove and *D. moneta* (37) has the prominence absent and the groove deeper, a condition almost identical with that of *Agraulis vanillae* (38, 39). *Heliconius isabella* (40) and *H. aliphera* (41) have only four tarsal segments, and the latter species also lacks the terminal spine. The way in which the fifth segment has been lost may be indicated by *H. ricini* (33), which exhibits an intermediate state with incomplete separation of tarsal segments one and two, though at this stage the stout ventral spines are still present, of which there are normally a pair on each segment with the exception of the most distal.

In all the female foretarsi examined there is a special association between the ventral spines and the specialized hairs which arise from circular areas of differentiated cuticle. The view that the female forelegs are functionless (Imms, 1957) should be qualified, for though unsuited to assist locomotion, the specialized arrangement of the hairs on the tarsi does not suggest a functionless organ. The investment of stout hairs and weak spines on the lateral and dorsal surfaces of the tarsi may be subject to specific arrangement, but it is very difficult to descale the tarsi without removing at least some of the spines as well, and once removed their origins are difficult to detect. Careful examination of *Philaethria* revealed no spinous structures on the proximal tarsal segment.

Meso- and Metathoracic Legs (Text-figs. 42, 43): The structure of the legs is orthodox, simi-



TEXT-FIGS. 3-20. Left view of left antennae of Heliconiinae. *Dryadula phaetusa*, 3; *Philaethria dido*, 4; *Agraulis vanillae*, 5; *Dryas iulia*, 6; *Podotricha telesiphe*, 7; *P. euchroia*, 8; *Dione moneta*, 9; *D. glycera*, 10; *D. juno*, 11; *Heliconius wallacei*, 12; *H. doris*, 13; *H. melpomene*, 14; *H. numata*, 15; *H. erato*, 16; *H. ricini*, 17; *H. sara*, 18; *H. isabella*, 19; *H. aliphera*, 20.



TEXT-FIG. 21. Left view of left male prothoracic leg of *Heliconius erato*.

TEXT-FIG. 22. Left view of left female prothoracic leg of *Dryas iulia*.

lar in both sexes, and shows no features of special interest except that *Dione* and *Podotricha* are alone in having hairs on the femora. In Trinidad Heliconiinae frequently have the translators of *Asclepias* (milkweed) attached to the spines of the meso- and metathoracic tibiae, and are presumably important pollinators of this wild herb.

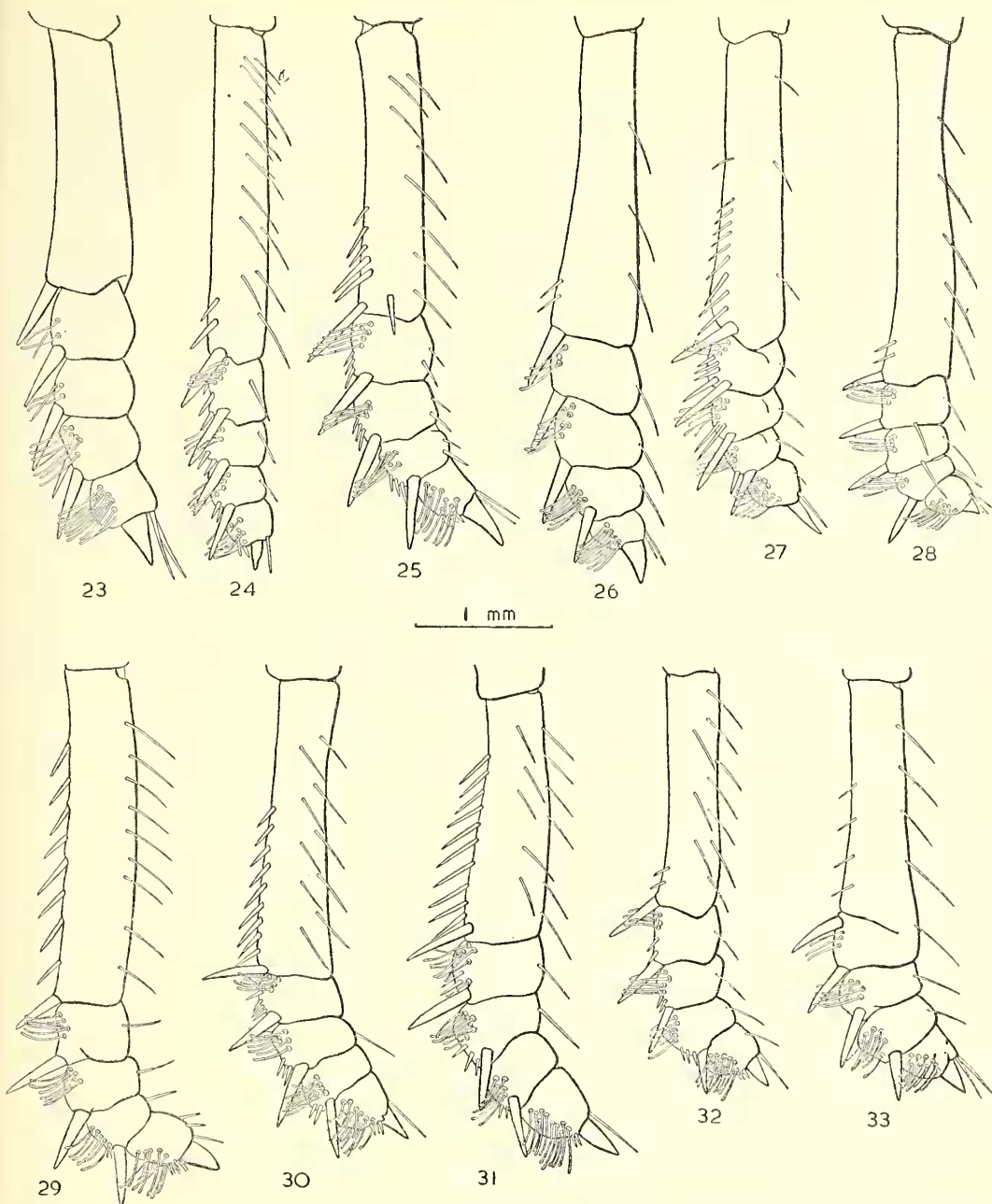
The pretarsi (Text-figs. 44-61) are similar on the meso- and metathoracic legs of both sexes. All genera except *Dione* and *Agraulis* have basically similar pretarsi with a pair of long curved claws, between which arise a large arolium and a pair of bifid paronychia. The dorsal and ventral processes of the paronychia (Text-fig. 45, Dpp and Vpp) exhibit variation in relative length, though the dorsal processes are consistently the more strongly sclerotized and are closely associated with the claws. In *Philaethria* (44), *Dryadula* (45), *Dryas* (46), *Podotricha* (47,48) and some species of *Heliconius* (49-52) the dorsal and ventral paronychial processes are nearly equal in length, whereas in the other species of *Heliconius* (53-55) they are widely different in length and in *Dione* (58-60) and *Agraulis vanillae* (61) the paronychia are vestigial.

In *H. numata* (49), *H. wallacei* (50), *H. melpomene* (51) and *H. doris* (52) the ventral paronychial processes are more than half as long as the dorsal processes but in *H. erato* (53), *H. sara* (54) and *H. ricini* (55) the ventral processes are less than a third as long as the dorsal ones. The paronychia of *H. isabella* (56) and *H. aliphera* (57) have much broader tips than any other species studied but are otherwise similar to other *Heliconius*, most particularly the group to which

H. numata belongs. *Dione junio* (58) and *Agraulis vanillae* (61) have a pair of similar, long, medially straight claws but lack the arolium and have poorly developed paronychial lobes. That the lobes are bifid in origin is shown more clearly in *D. glycera* (59) and *D. moneta* (60). Pretarsal differentiation can be expected to be closely adapted to specific habits and are probably among the less useful taxonomic characters for establishing interrelationships, but from field observations no habits common to *Agraulis* and *Dione*, which differ from the remainder of the Heliconiinae, have been observed.

The wings (Text-figs. 62-80) of Heliconiinae are recognised by their high aspect ratio, though this is pronounced only in *Podotricha* (65, 66), *Dryas* (67) and *Heliconius* (70-78). Genera like *Dryadula* (69) are nearer the normal nymphaline proportions. The wings may have rounded distal margins as in *Dryadula* (69), *Agraulis* (68) and most species of *Heliconius* (70-78) or they may be scalloped as in *Dione* (63-64) and some other species of *Heliconius* not figured. The substantial emargination of the forewing of *Podotricha* (65-66) in the region of M3 and Cu1a may be seen developed to a lesser extent in *Dione* (63-64) and is just perceptible in *Philaethria* (62), *Dryas* (67) and *Agraulis* (68).

The venation (Text-figs. 62-80) of the Heliconiinae is unique for the exhibition on the hindwing of an unforked recurrent humeral branch of Sc. The subfamily may be divided into two groups, for though in all genera the discal cell of the forewing is closed by the crossveins M2-M3 and M3-Cu1a (Text-figs. 67, 74), only in *Heliconius* is the crossvein M2-M3 present on the hindwing too (Text-fig. 74). The absence of this crossvein in the other genera leaves the discal cell open (Text-fig. 67). The extent to which the vestiges of the stems of R4 + R5 and M are visible in the adult forewing is subject to considerable variation in each species, but in all cases only the base of Cu2 can be identified, and on the hindwing all trace of the base of M and Cu2 has been lost, except Cu2 in some specimens of *H. numata* (71). The homologies of the veins labelled in the drawings of *Dryas iulia* (67) and *Heliconius erato* (74) can be confirmed by reference to the pupal tracheations which are shown in Text-figs. 79 and 80. In the past, taxonomic use has been made of the point of origin of R1 of the forewing relative to the anterodistal angle of the discal cell, but it is not a good character as it is subject to considerable variation and even the sexual dimorphism of *Agraulis* cited by Michener (1942a) cannot be substantiated. This variation is not surprising, for the pupal tracheation shows a complex association

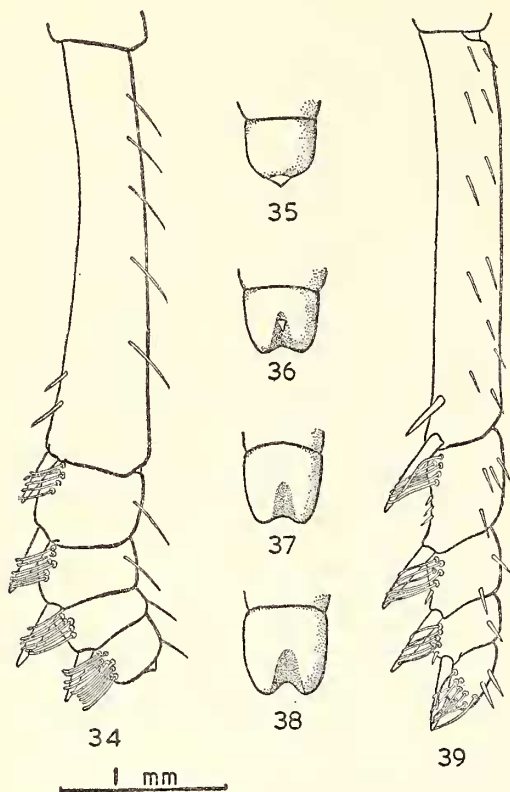


TEXT-FIGS. 23-33. Right view of right prothoracic leg of female Heliconiinae. *Philaethria dido*, 23; *Dryadula phaetusa*, 24; *Dryas iulia*, 25; *Podotricha telesiphe*, 26; *Heliconius numata*, 27; *H. wallacei*, 28; *H. doris*, 29; *H. melpomene*, 30; *H. erato*, 31; *H. sara*, 32; *H. ricini*, 33.

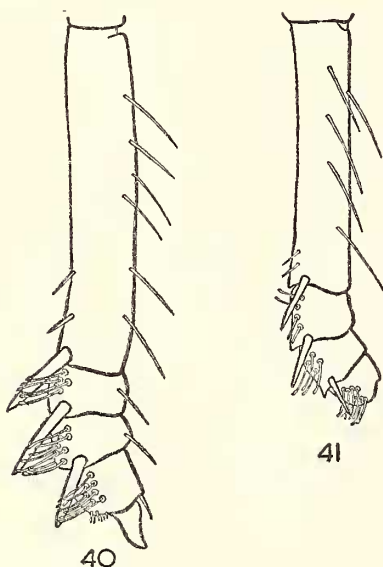
of trachea in this region (Text-figs. 79 and 80) and the critical point is where the tracheae which precede R2 + 3 and R4 + 5 first meet. Apart from the separation of *Heliconius* by the closure of the discal cell on the hindwing, the only other venational feature of systematic interest is the

similarity of the unusual course of Sc + R1 and M2 in *Dione glycera* and *D. moneta* which is associated with the pattern of silver spots on the ventral surface; *D. juno* is almost unmodified in this respect.

The androconia (Text-figs. 81-92) of nearly



TEXT-FIGS. 34-41. Right view of right prothoracic leg of female Heliconiinae. *Dione juno*, 34, 35; *D. glycera*, 36; *D. moneta*, 37; *Agraulis vanillae*, 38, 39; *Heliconius isabella*, 40; *H. alipha*, 41.

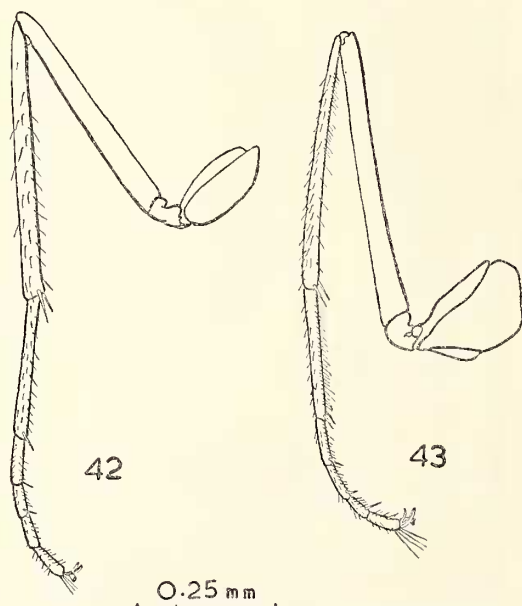


all the genera can be distinguished by their shape, though their basic structure seems uniform. The odor-disseminating region is probably confined to the distal zone where the scales are finely divided and highly refractive. *Dryadula* (88), *Dryas* (hindwing) (89), and *Heliconius* (90-92) are similar in having squat rectangular androconia, and those of *isabella* (92) and *H. alipha* are almost square.

The androconia of *Agraulis vanillae* (81), *Dione moneta* (82), *D. glycera* (83), *D. juno* (84), *Dryas iulia* (forewing) (85), *Podotricha* (86), *Philaethria dido* (87), *Dryadula phaetusa* (88) and *Heliconius* (90-92) form a series which decreases regularly in length. The androconia of some Heliconiinae were studied and figured by Müller (1877a; 1877b). *Dryas* is especially interesting as the forewing androconia are elongate and similar to those of *Philaethria*, *Podotricha* and *Dione juno*, whereas the androconia of the hindwing are short and similar to those of *Heliconius* and have a similar distribution.

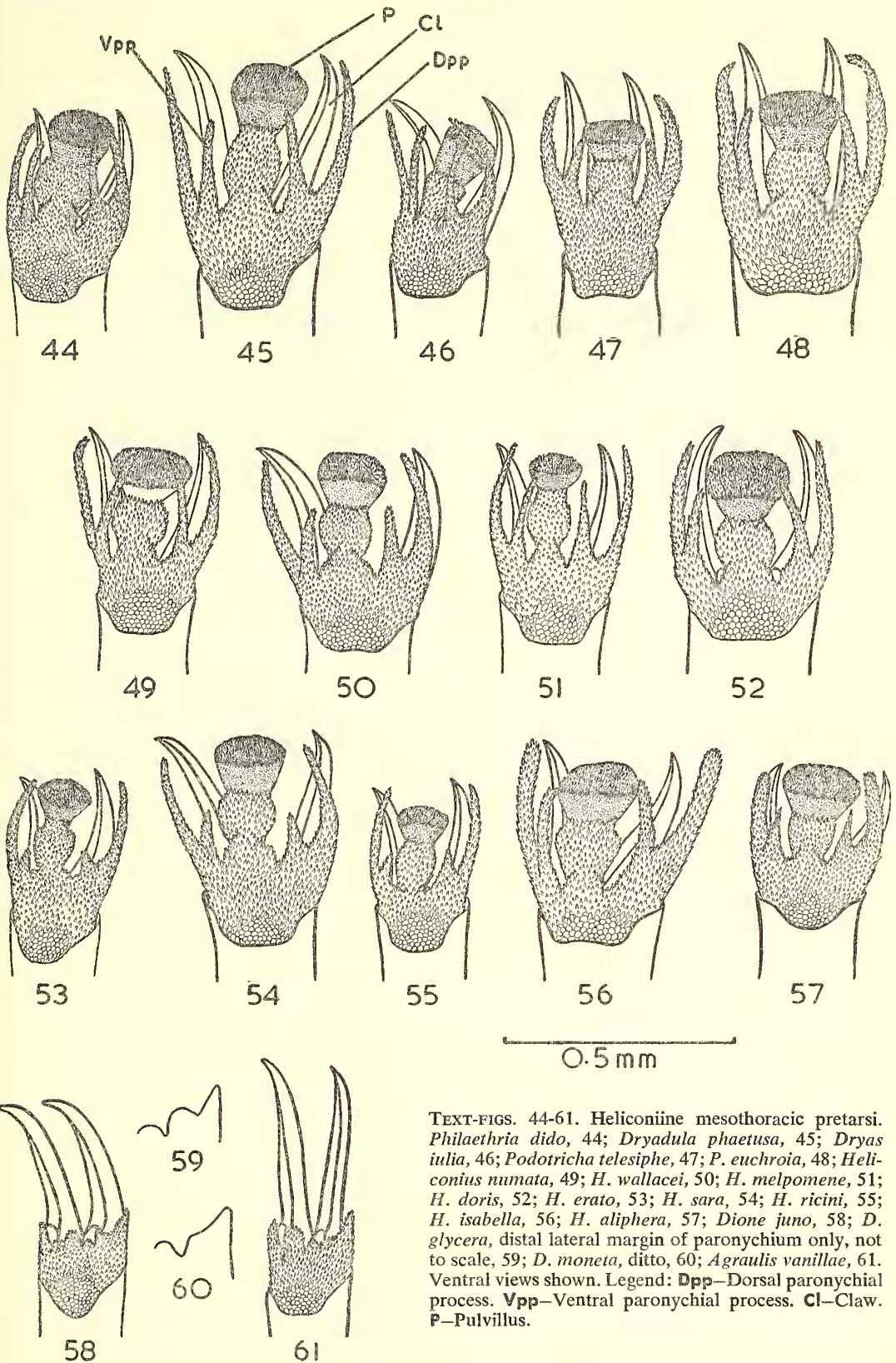
The distribution of the androconia (Text-figs. 62-78) on the wings of male Heliconiinae is an important systematic character and will be described first under each genus and then as a whole.

In *Philaethria dido* (62), all the distal veins of the forewings except C, Sc, R1, and R2, and

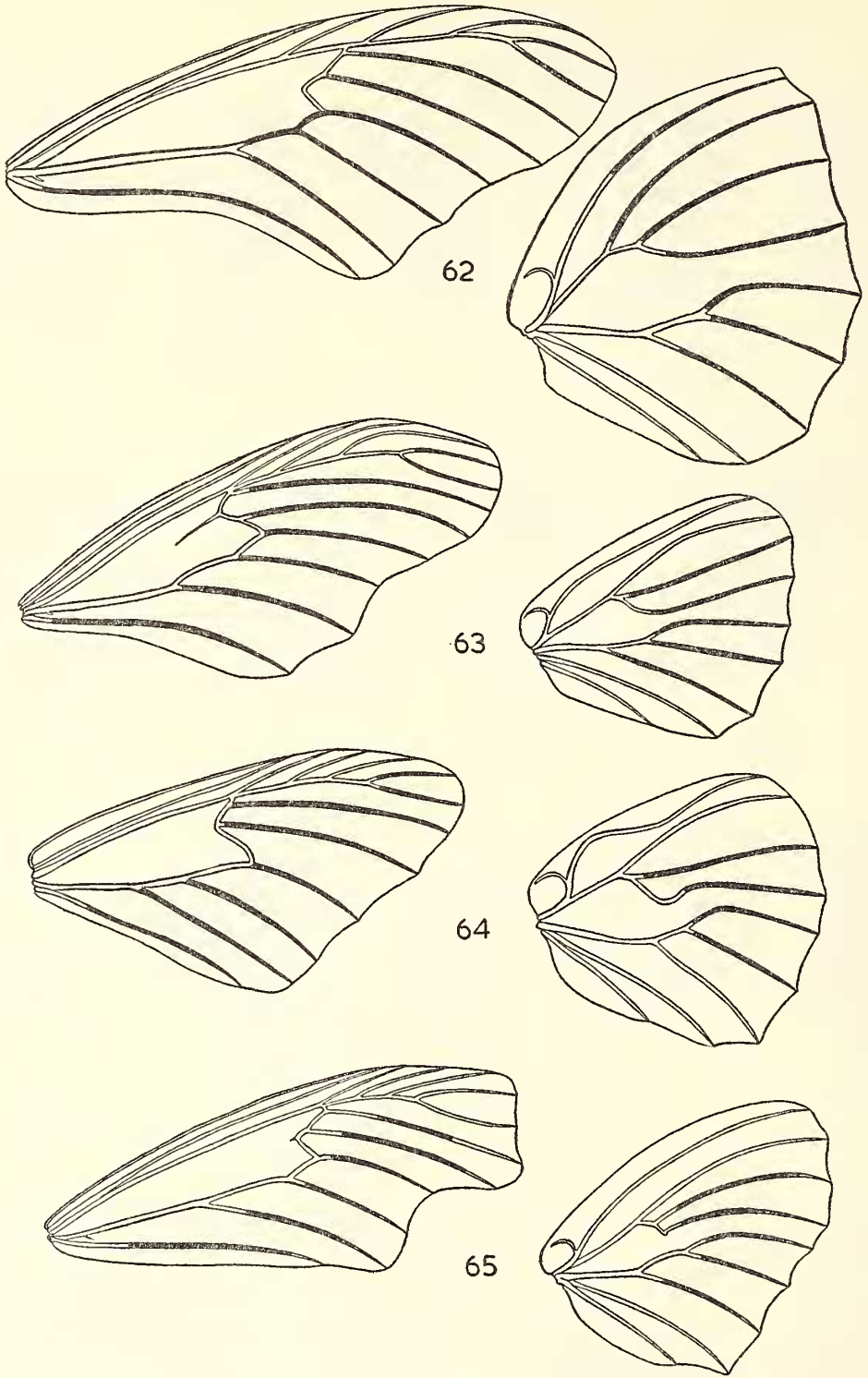


TEXT-FIG. 42. Right view of right mesothoracic leg of *Dryas iulia*.

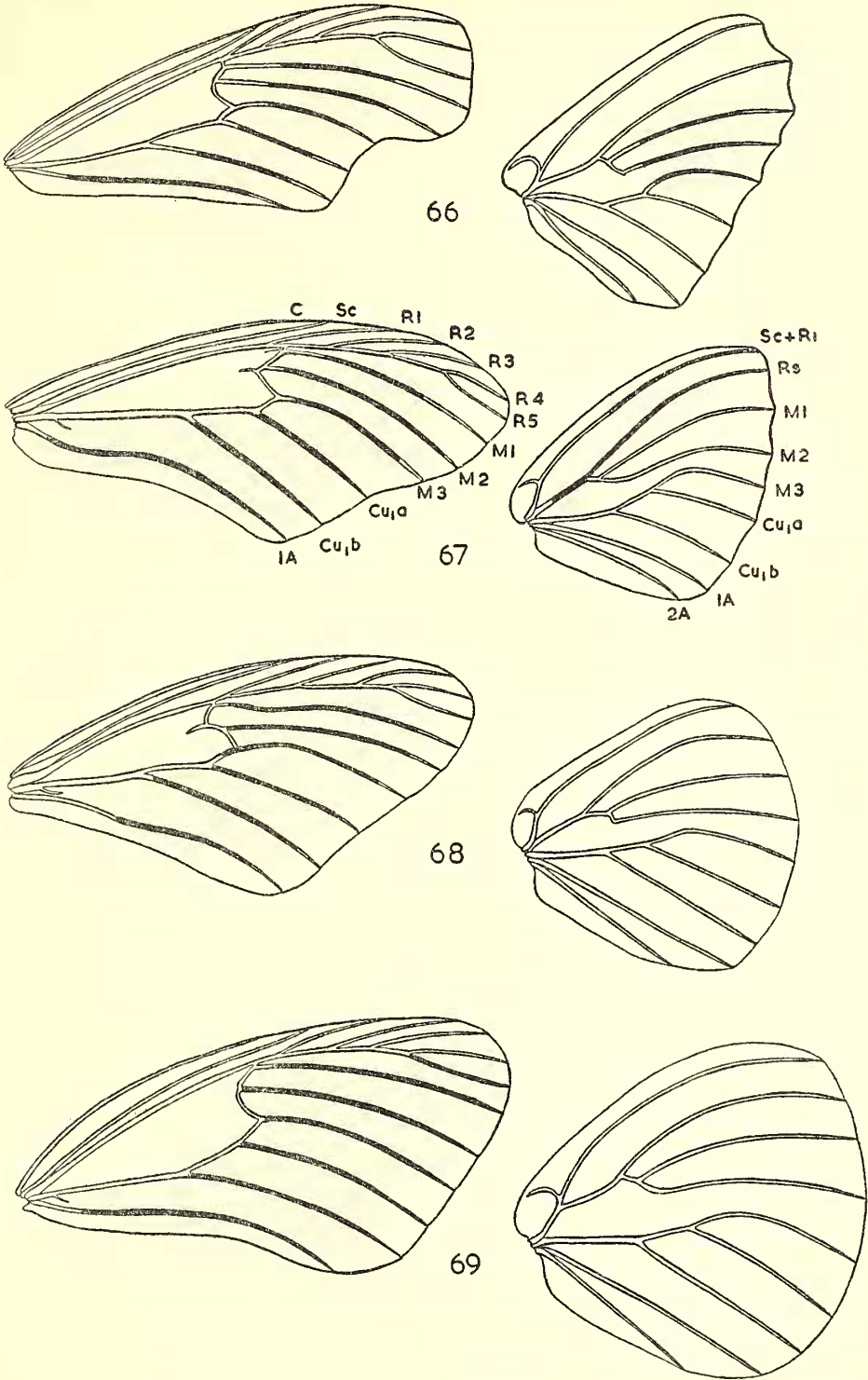
TEXT-FIG. 43. Right view of right metathoracic leg of *Dryas iulia*.



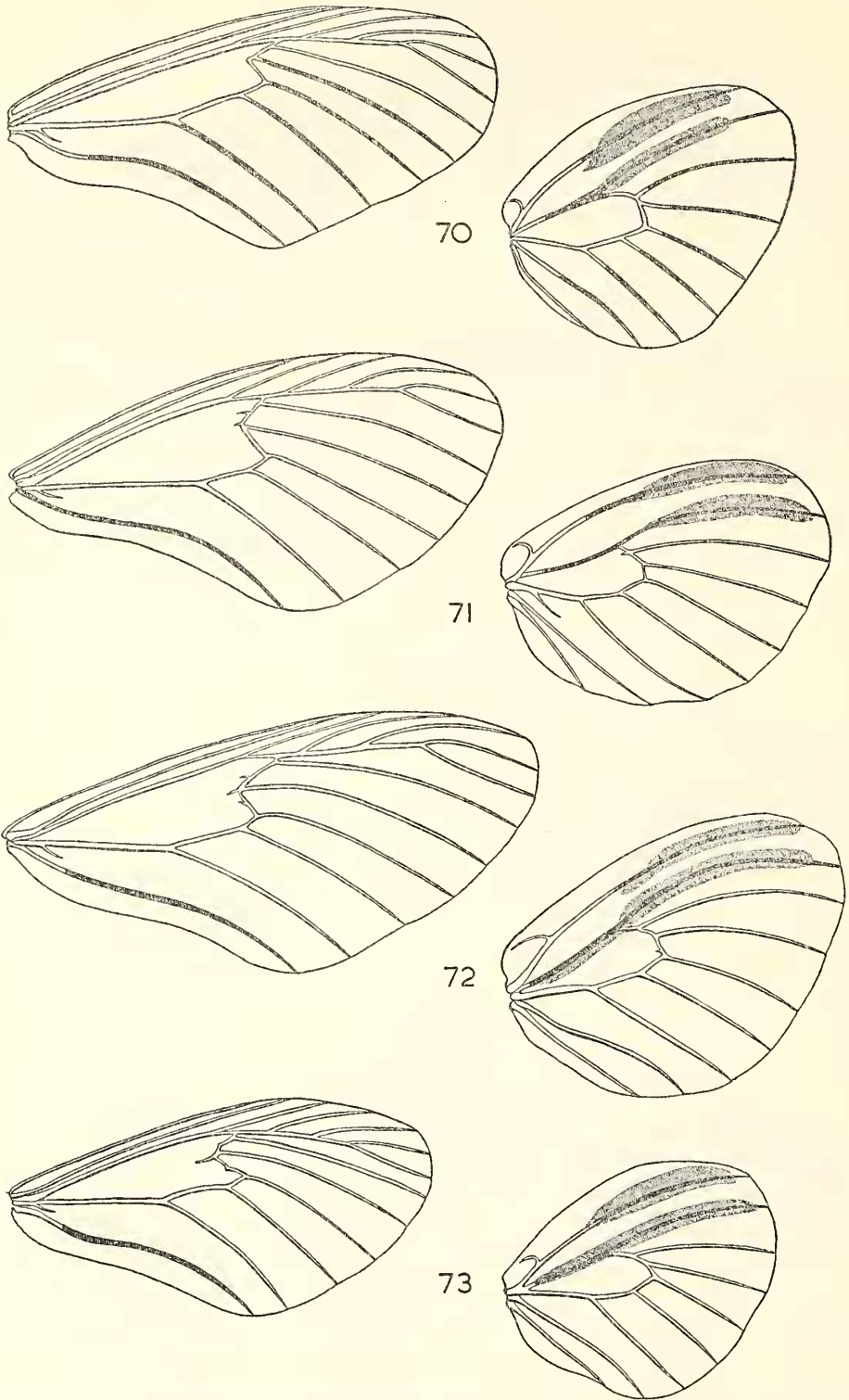
TEXT-FIGS. 44-61. Heliconiine mesothoracic pretarsi. *Philaethria dido*, 44; *Dryadula phaetusa*, 45; *Dryas iulia*, 46; *Podotricha telesiphe*, 47; *P. euchroia*, 48; *Heliconius numata*, 49; *H. wallacei*, 50; *H. melpomene*, 51; *H. doris*, 52; *H. erato*, 53; *H. sara*, 54; *H. ricini*, 55; *H. isabella*, 56; *H. aliphera*, 57; *Dione junco*, 58; *D. glycera*, distal lateral margin of paronychium only, not to scale, 59; *D. moneta*, ditto, 60; *Agraulis vanillae*, 61. Ventral views shown. Legend: **Dpp**—Dorsal paronychial process. **Vpp**—Ventral paronychial process. **Cl**—Claw. **P**—Pulvillus.



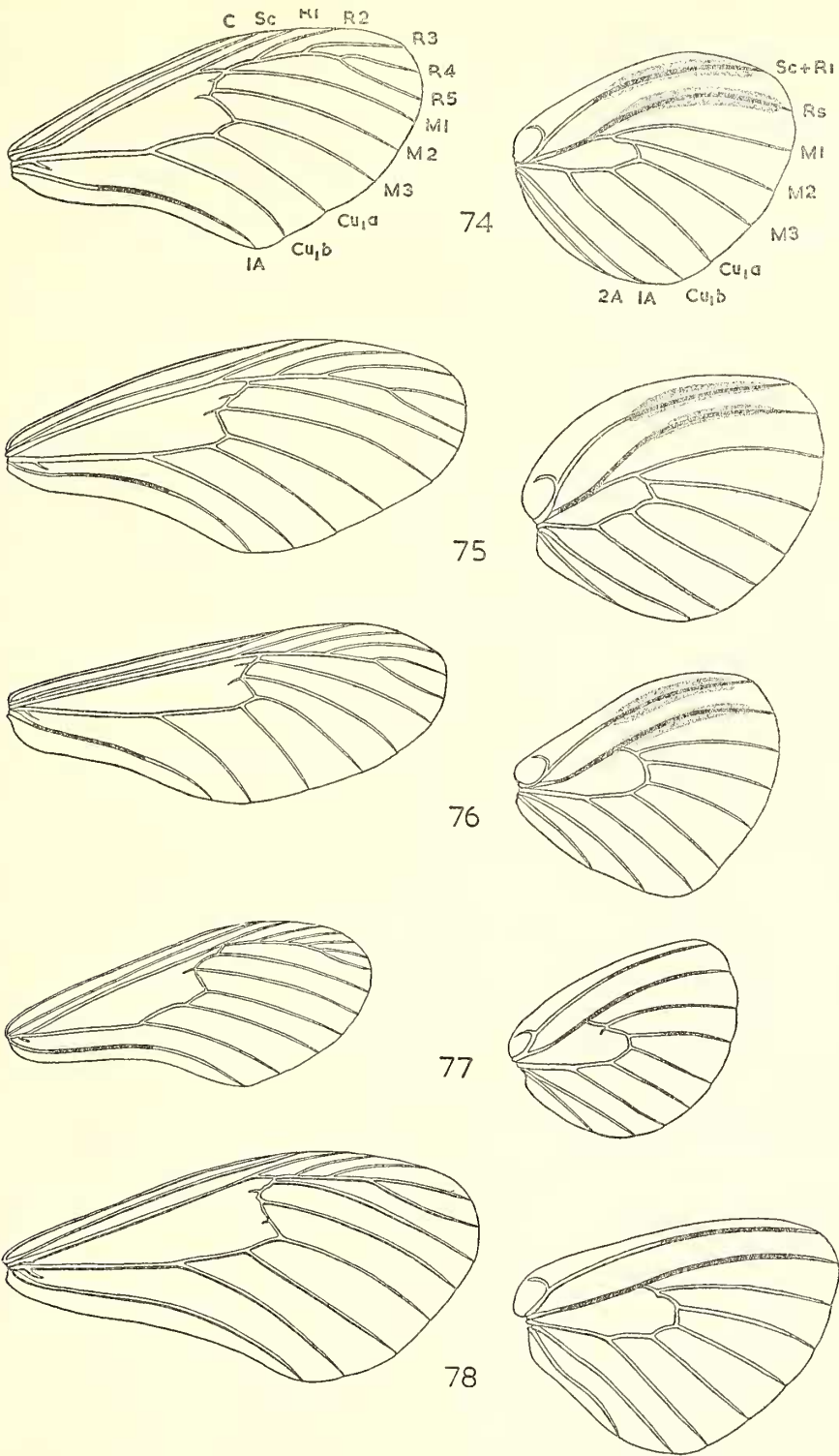
TEXT-FIGS. 62-65. Dorsal view of right fore and hind wings of Heliconiinae. Twice natural size. Androconia are shown as solid black lines on the veins. *Philaethria dido*, 62; *Dione juno*, 63; *D. glycera*, 64, *D. moneta* similar; *Podotricha euchroia*, 65.



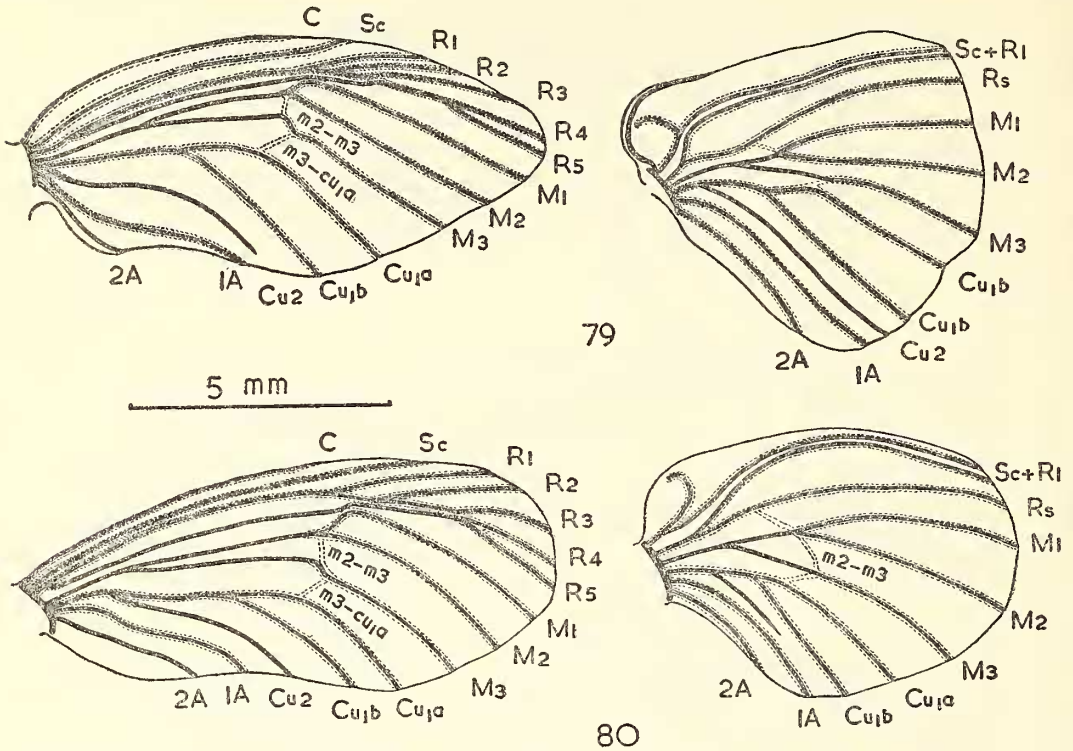
TEXT-FIGS. 66-69. Dorsal view of right fore and hind wings of Heliconiinae. Twice natural size. Androconia are shown as solid black lines on the veins. *P. telesiphe*, 66; *Dryas iulia*, 67; *Agraulis vanillae*, 68; *Dryadula phaetusa*, 69.



TEXT-FIGS. 70-73. Dorsal view of right fore and hind wings of Heliconiinae. Twice natural size. Androconia are shown on the veins in black, and on the membrane stippled. *Heliconius wallacei*, 70; *H. numata*, 71; *H. doris*, 72; *H. melpomene*, 73.



TEXT-FIGS. 74-78. Dorsal view of right fore and hind wings of Heliconiinae. Twice natural size. Androconia are shown on the veins in black, and on the membrane stippled. *H. erato*, 74; *H. sara*, 75; *H. ricini*, 76; *H. aliphera*, 77; *H. isabella*, 78.



TEXT-FIG. 79. Pupal wing pads of *Dryas iulia* showing tracheae as solid lines and the adult venation dotted. Forewing on left, hindwing on right.

TEXT-FIG. 80. Pupal wing pads of *Heliconius erato* showing tracheae as solid lines and the adult venation dotted. Forewing on left, hindwing on right.

all the distal veins of the hindwings except 1A and 2A have androconia along almost their whole length. This is contrary to the statement by Michener (1942a) that androconia are absent on the wing veins. For the nomenclature of the venation see the wings of *Dryas iulia* (Text-fig. 67).

The distribution of androconia in *Dione juno* (63) is similar to that of *P. dido* except that they are also absent on R3 of the forewings, and Sc + R1 and Rs on the hindwings. In *D. glycera* (64) and *D. moneta*, androconia are absent from hindwing Cu1b as well.

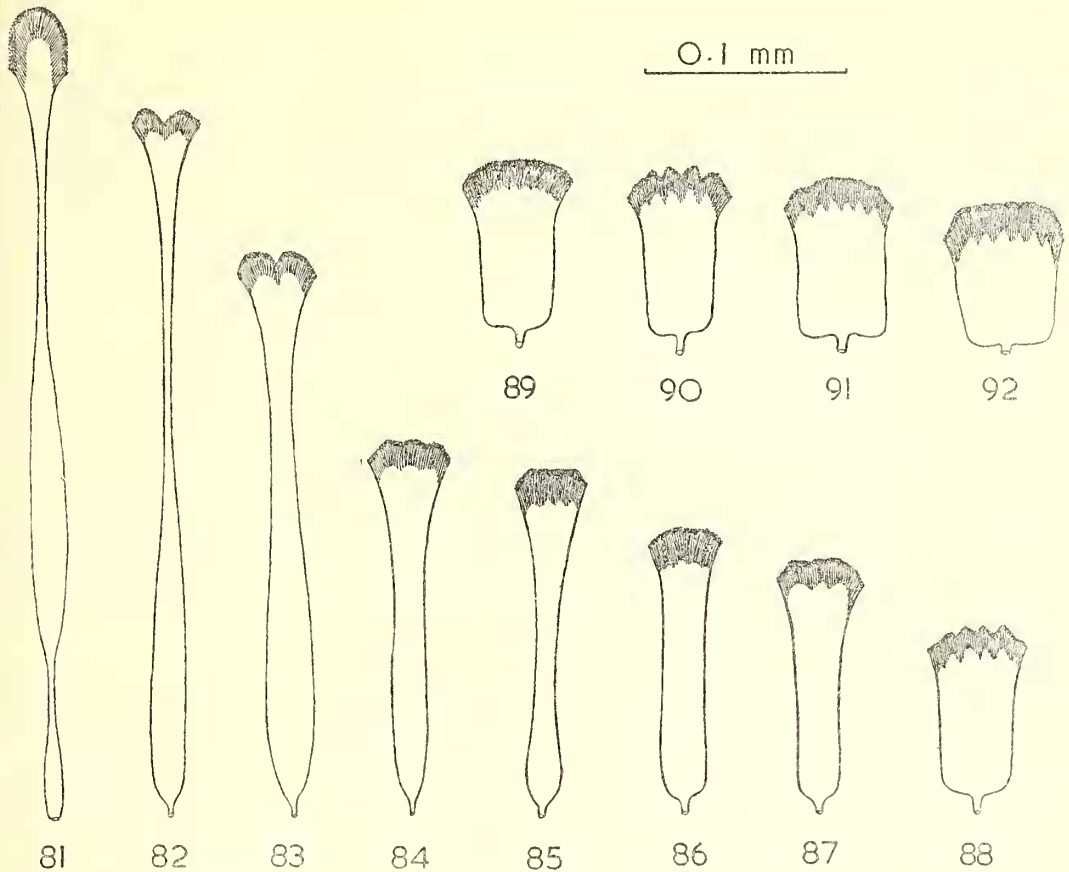
On the forewings of *Podotricha* (65, 66), androconia are present only on veins M1, M2, M3, Cu1a, Cu1b and 1A, and on the hindwings *P. euchroia* has them on wingveins M1, M2, M3, Cu1a and Cu1b, and *P. telesiphe* only on veins M1, M2, and M3. Only vein 1A of the forewing has a heavy investment of androconia; on the remaining veins of both pairs of wings they are very sparse indeed.

In *Dryadula phaetusa* (69), androconia occur on all the forewing veins except C, Sc, R1, R2,

R3 and R4 and are entirely absent from the hindwing. Michener (1942a) overlooked the androconia.

The distribution of androconia in *Agraulis vanillae* (68) is similar to that of *Dryadula* except they are also absent from R5 of the forewing.

There is geographic differentiation in the distribution of the forewing androconia of *Dryas* (67), an account of which is given under the Systematic Synopsis. On the continental forms, androconia are present only upon forewing veins Cu1a, Cu1b and 1A and on hindwing veins Sc + R and Rs, but some Greater and Lesser Antillean specimens have androconia also on forewing veins M1, M2 and M3. It is likely that the inheritance of the androconial pattern is controlled by a simple genetic mechanism. In addition to the forewing androconia, they are present also on the two anterior hindwing veins Sc + R1 and Rs, and their arrangement in transverse rows which alternate with normal scales produces an effect very similar to that seen in *Heliconius*, which also has androconia on these veins.



TEXT-FIGS. 81-92. Heliconiine androconia: *Agraulis vanillae*, 81; *Dione moneta*, 82; *D. glycera*, 83; *D. juno*, 84; *Dryas iulia* forewing, 85; *Podotricha euchroia*, 86; *Philaethria dido*, 87; *Dryadula phaetusa*, 88; *Dryas iulia*, hindwing, 89; *Heliconius numata*, 90; *H. wallacei*, 91; *H. isabella*, 92.

In most of the species of *Heliconius* studied for this paper, androconia are confined to veins Sc + R1 and Rs of the hindwing, on the neighboring membrane and on vein 1A of the forewing, but *H. wallacei* (70) and some species allied to *numata*, but not represented in Trinidad, have in addition androconia on forewing veins M2, M3, Cu1a and Cu1b and hindwing veins M1, M2, M3, Cu1a, Cu1b and sometimes 1A. The androconia that can be found occasionally on the posterior margin of the forewing have probably been dislodged from the hindwing. Michener (1942a) does not describe androconia in *Heliconius*. The species available in Trinidad fall into five groups.

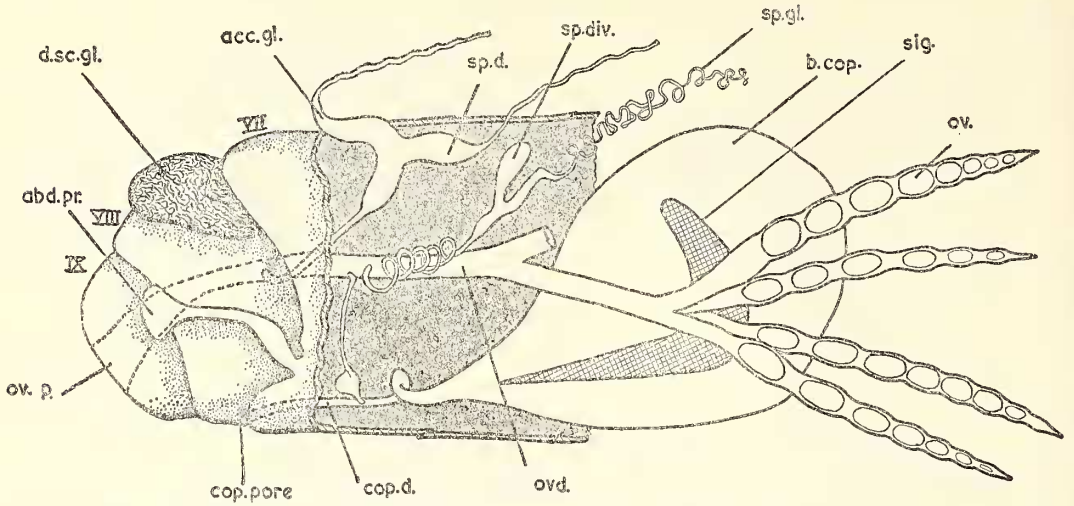
(a) Those which have a dense investment of androconia on hindwing veins Sc + R1 and Rs, and over a substantial portion of the membrane around them; have some androconia on other hindwing veins; and on some forewing veins additional to 1A. *H. wallacei* (70) is the only representative of this group from Trinidad.

(b) Those with a dense investment of androconia only on hindwing veins Sc + R1 and Rs and on the membrane around them, and on forewing vein 1A; *Heliconius numata* (71), *H. doris* (72) and *H. melpomene* (73) belong to this group.

(c) Those with a distribution similar to (b) but in which the investment of androconia on the membrane around Sc + R1 and Rs is more restricted and much less dense, emphasizing the contrast between vein and membrane. The androconia on 1A of the forewing are also less obvious. *H. erato* (74), *H. sara* (75) and *H. ricini* (76) belong to this group.

(d) Those with androconia only on hindwing veins Sc + R1 and M and Cu. There are no androconia on the membrane. *H. aliphira* (77) is the only representative from Trinidad.

(e) Those with the androconia restricted entirely to veins Sc + R1 and Rs of the hind-



TEXT-FIG. 93. Generalized diagram of female reproductive system and female abdominal scent glands and processes. Legend: *acc. gl.*—accessory gland; *d. sc. gl.*—dorsal scent gland; *abd. pr.*—abdominal process; *cop. p.*—copulatory pore; *cop. d.*—copulatory duct; *ovd.*—oviduct; *ov.*—ovariole; *ov. p.*—oviducal pore; *sig.*—signum; *b. cop.*—bursa copulatrix; *sp. gl.*—spermatheca gland; *sp. div.*—spermathecal diverticulum; *sp. d.*—spermathecal duct.

wing. *H. isabella* (78) is the only Trinidad representative.

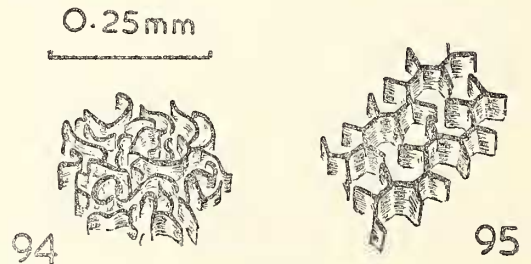
Assuming that the most complete pattern, as exhibited by *Philaethria* (62), is primitive, then ignoring minor variations, the distribution of androconia in *Dryadula* (69) and *Agraulis* (68) can be achieved by the loss of androconia from the hindwing veins. The condition in *Dione* (63, 64) and *Podotricha* (65, 66) can be achieved by the loss of androconia on hindwing veins Sc + R1 and Rs, and that of *Dryas* (67) by the loss of androconia on all the hindwing veins except Sc + R1 and Rs. That the genetic constitution of the Heliconiinae is compatible with the suggestion that discrete groups of veins can lose their androconia is supported by the variation demonstrated by the forewings of *Dryas*. *Heliconius* (70-78) shows some diversity in distribution but they all have in common the alternate transverse rows of dense androconia on hindwing veins Sc + R1 as in *Dryas*.

ABDOMEN

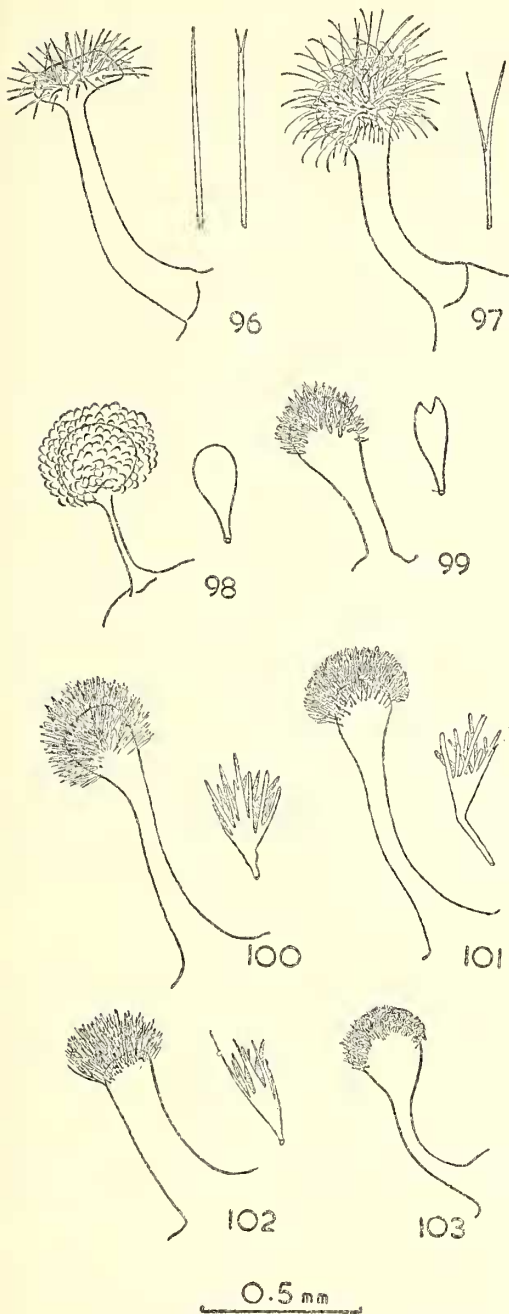
The female scent glands (Text-figs. 93-103) are the principal structures of interest on the pregenital abdominal segments and characterize the subfamily. They are medianly divided structures which are a development of the dorsal membrane separating abdominal segments eight and nine (Text-fig. 93). The glands consist of a pair of highly infolded cuticular pouches whose lining is presumably secretory, and which are capable of eversion, apparently by hydraulic

pressure. The exposed surface of the gland is highly sculptured, presumably to increase the surface area (Text-figs. 94, 95). There are at least generic differences in gland sculpture but the difficulties of preparation and accurate interpretation make them unreliable for systematic purposes.

The females of *Philaethria dido* (98), *Dryas iulia* (99), *Agraulis vanillae* (97), *Dione* (96), *Podotricha* and *Heliconius* each have a pair of ventro-lateral processes developed from the posterior margin of the eighth segment which project dorsally (Text-fig. 93), and which in repose lie within the dorsal scent glands. The processes are not articulated at their base but are rigid outgrowths of the sternum, and with ventral flexing of the abdomen the capitate heads are withdrawn from the gland. The shape of the processes and their clothing of scales show generic



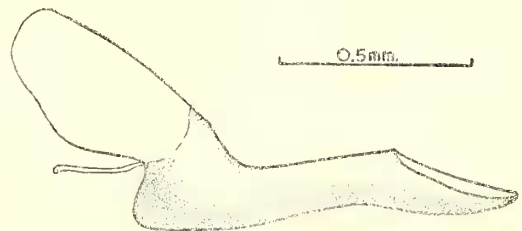
TEXT-FIGS. 94 & 95. Detail of infolding of female dorsal abdominal glands. *Dryadula phaetusa*, 94; *Dryas iulia*, 95.



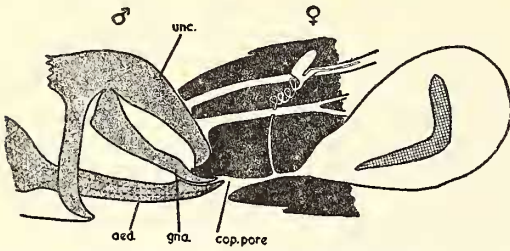
TEXT-FIGS. 96-103. Abdominal processes of female Heliconiinae. Details of specialized scales inset to right. *Dione juno*, 96; *Agraulis vanillae*, 97; *Philaethria dido*, 98; *Dryas iulia*, 99; *Heliconius melpomene*, 100; *H. isabella*, 101; *H. sara*, 102; *H. erato*, 103.

features, some of which are figured by Müller (1878). In *Philaethria dido* (Text-fig. 98) the process is short with a spherical tip, densely clothed with scales which are entire and bladder-like. *Dryas iulia* (99) has a more club-shaped process with a more sparse clothing of laterally flattened apically dentate scales. *Dione juno* (96), *moneta*, and *glycera*, *Podotracha euchroia* and *telesiphe* and *Agraulis vanillae* (97) are similar in that the processes are strongly capitate with a slender pedicel and the scales are excessively elongate and hair-like. The deeply bifid condition of *A. vanillae* is developed to a lesser extent in many of the scales of *Dione*, but the scales of *Podotracha* are unbranched. *Heliconius* (100-103) shows considerable diversity in the shape of the processes but in all the species studied the scales are like an inverted hollow cone with deeply divided walls. *Dryadula phaetusa* has no processes, though the dorsal scent glands are more highly developed. The complement of scales on the capitate heads of the processes varies according to whether they are examined before or after copulation, for during copulation the appendages are withdrawn from the scent glands by the depression of the tip of the abdomen and fit into grooves on the inner face of the male genital valves; this may be an involuntary movement due to the depression of the abdomen during copulation.

The male genitalia (Text-figs. 104-123) has in the past been the chief non-alary character used in papilionoidian taxonomy, though the interpretation to be placed on the diversity of valvular form is only recently becoming understood. Studies like those of Lorković (1956) and Turner, Clarke & Sheppard (1961) are rejecting the lock and key concept of the function of the valves. Examination of specimens electrocuted in the act of copulation, using the technique described by Emsley (1958), shows clearly that it is the uncus and gnathos (Text-fig. 105) that are the principal grasping organs together with the inflatable tip of the aedeagus (Text-fig. 104). The inflatable pouches at the base of the valves are in intimate contact with the female but seem to have a function other than that of



TEXT-FIG. 104. Left view of aedeagus of *Dryadula phaetusa* to show obliquely truncate tip.

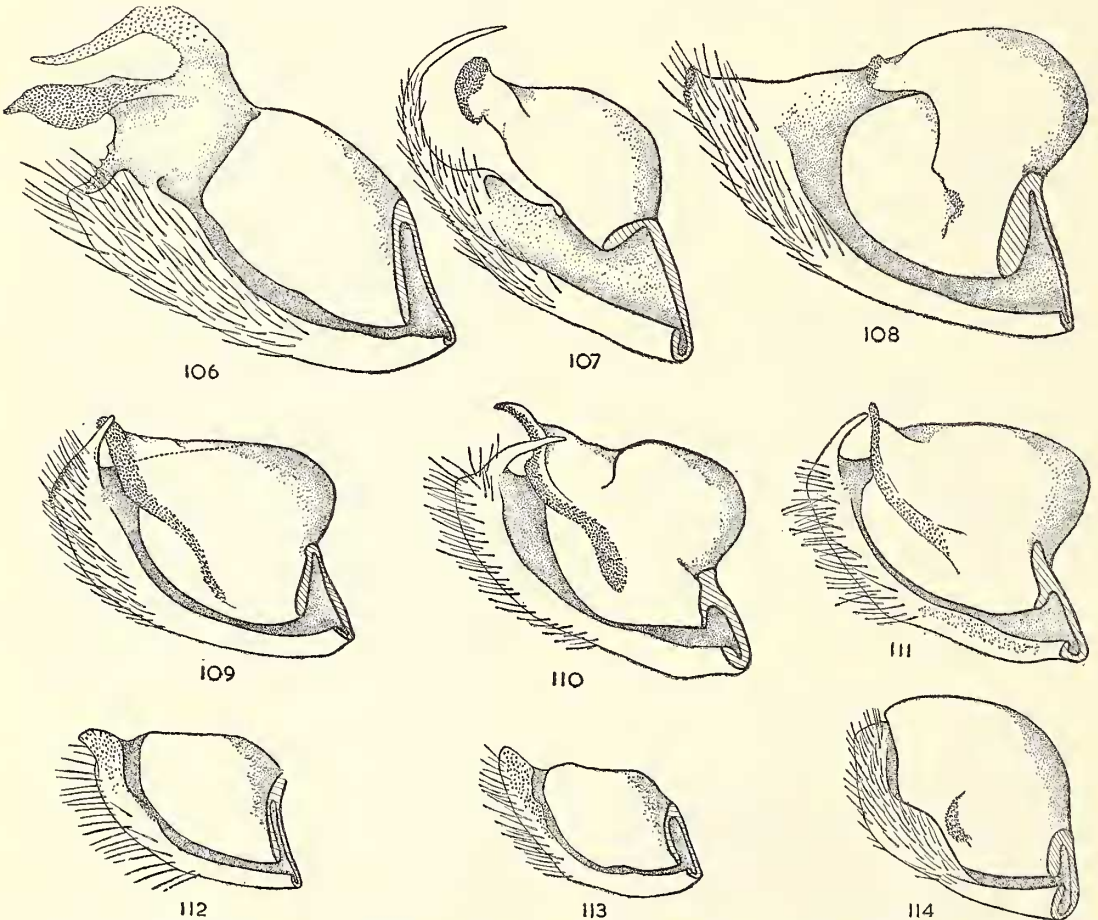


TEXT-FIG. 105. Diagram to illustrate mechanism of copulation. Legend. Aed.—aedeagus; Cop. pore—copulatory pore; gna.—gnathos; unc.—uncus.

prehension. The distal portions of the valves of the male have little or no contact with the female and are independently free to exploit genetic variability, hence the development of the bizarre extremities exhibited by *Dryadula* (106) and *Philaethria* (107). That this is the method of

copulation could have been deduced from the manipulation of living and preserved material, for the uncus is flattened laterally for insertion into the female egg pore, and the gnathos is flattened dorso-ventrally to grasp the roof of the copulatory pore, which is locally heavily sclerotized. The aedeagus (104) is obliquely truncate and fits closely against the lower surface of the gnathos, which acts as a guide for its introduction into the copulatory pore (105). The aedeagus is inserted approximately three-quarters of the length of the ductus bursa, the remaining distance being accomplished by eversion of the lining of the ejaculatory duct, which expands within the bursa copulatrix and assists in preventing accidental withdrawal. *Dryas iulia* is peculiar in that it has at the dorsal tip of the aedeagus a group of approximately ten strong spines whose function is unknown.

The male genital valves (Text-figs. 106-123).



TEXT-FIGS. 106-114. Inner aspect of left genital valves of male Heliconiinae. *Dryadula phaetusa*, 106; *Philaethria dido*, 107; *Agraulis vanillae*, 108; *Dione juno*, 109; *D. glycera*, 110; *D. moneta*, 111; *Podotricha euchroia*, 112; *P. telesiphe*, 113; *Dryas iulia*, 114.

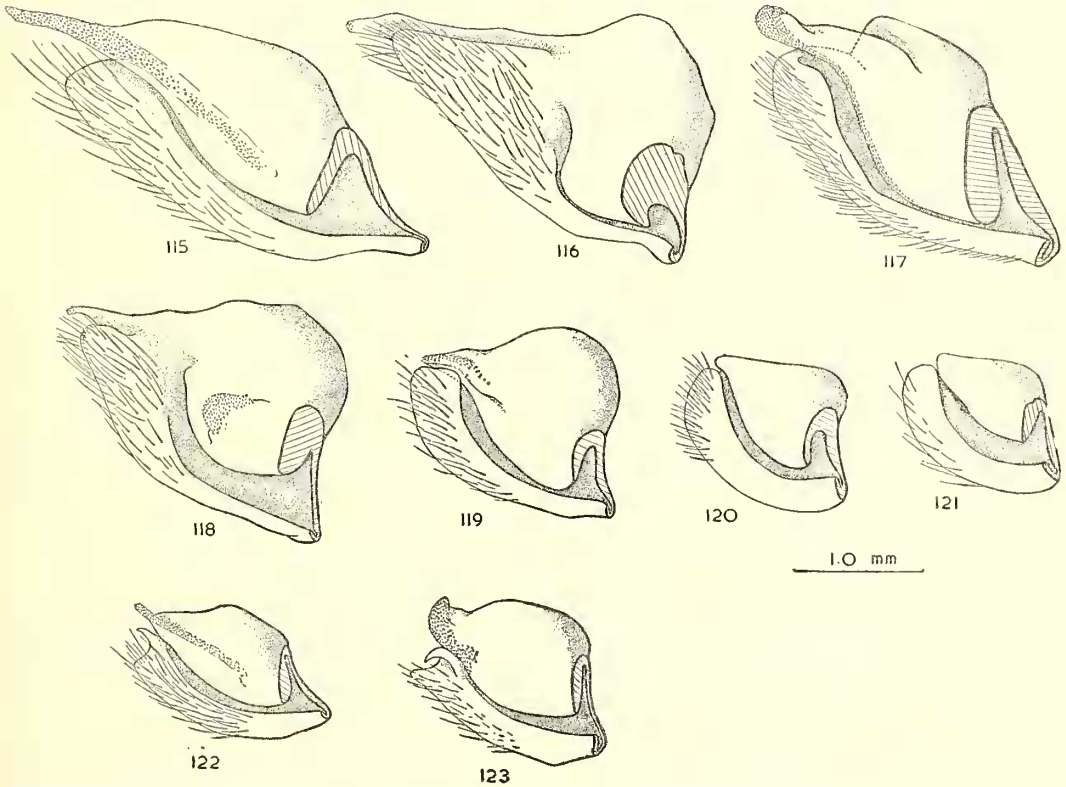
From a study of the valves, the erection by Michener of numerous genera seems justified, particularly in view of the similarities within genera like *Dione* (109-111) and *Podotricha* (112-113). Though in general the valves do not suggest intergeneric relationships, there is a striking similarity between the *Heliconius* type of valve (e.g., 119-121) and that of *Dryas iulia* (114), and they are of considerable value in erecting species groups. Within *Heliconius* three groups can be recognized. Firstly: *H. wallacei* (115), *H. numata* (116), *H. doris* (117) and *H. melpomene* (118), are united by the elongate and spinose development of the dorsal process of the valve which makes it considerably longer than the conical and smooth ventral process. Secondly: *H. erato* (119), *H. sara* (120), and *H. ricini* (121) have the dorsal process reduced and smooth so the rounded ventral process is the more prominent, though *H. erato* approaches the condition seen in *melpomene*. Thirdly: *H. aliphera* (122) and *H. isabella* (123) have both the upper and lower processes approximately equally developed but the lower process is, or has a tendency to be, bifid. These

two species each have a spinose region on the inner surface of the dorsal process, a feature not developed in the *H. erato*, *H. sara*, *H. ricini* group, but which is seen in some other species of *Heliconius*, like *H. wallacei*, and in *Dione*.

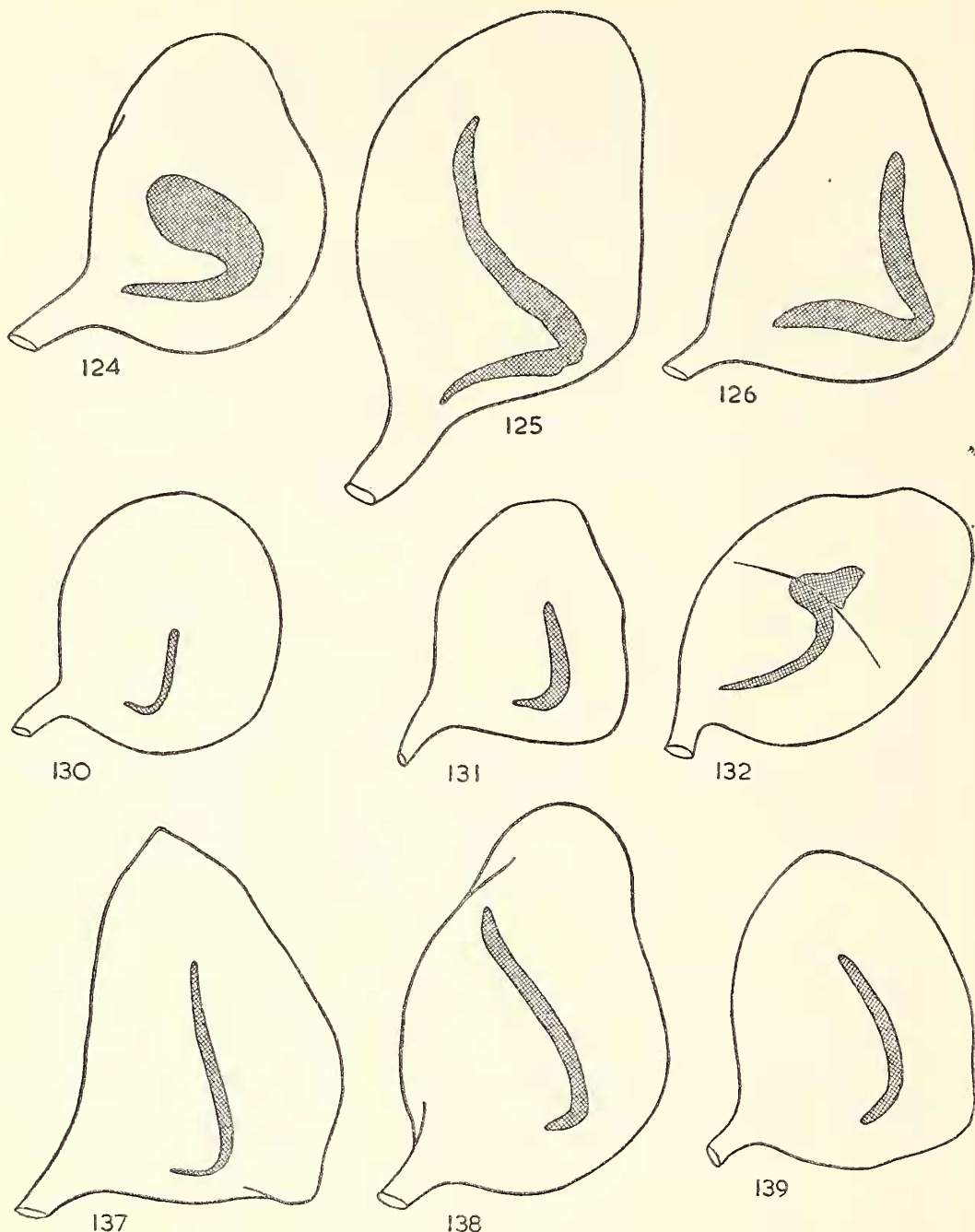
No characters of systematic value were detected on the other components of the male genitalia.

The female genitalia (Text-figs. 93, 124-152) of ditrysic lepidoptera include internal ectodermal structures which are lined with cuticle. The relationships of the component parts are illustrated in Text-fig. 93. The important features are the bursa copulatrix (b. cop), into which the sperm are deposited as a spermatophore during copulation; the spermatheca (sp.d.), to which the sperm migrate after the rupture of the spermatophore; and a pair of accessory glands (acc. gl.) which are responsible for the secretion of the adhesive which secures the egg to the substrate.

The bursa copulatrix has a shape which is subject to considerable variation in each species due to its state at the time of the capture of



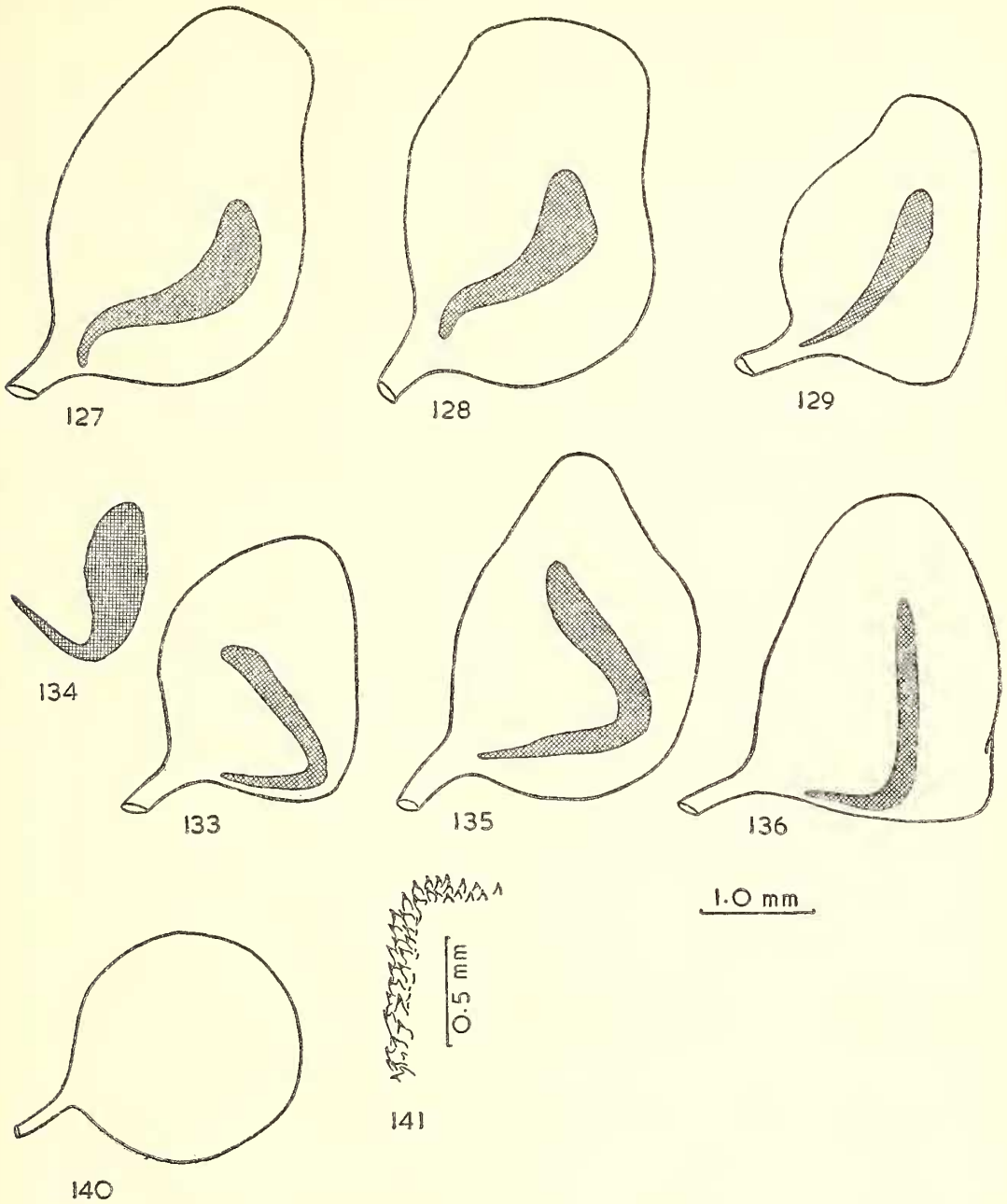
TEXT-FIGS. 115-123. Inner aspect of left genital valves of male Heliconiinae. *Heliconius wallacei*, 115; *H. numata*, 116; *H. doris*, 117; *H. melpomene*, 118; *H. erato*, 119; *H. sara*, 120; *H. ricini*, 121; *H. aliphera*, 122; *H. isabella*, 123.



TEXT-FIGS. 124-126, 130-132, 137-139. Right view of bursa copulatrix of Heliconiinae. The right signum is shaded. *Philaethria dido*, 124; *Dryadula phaetusa*, 125; *Dryas iulia*, 126; *Podotricha euchroia*, 130; *P. telesiphe*, 131; *Agraulis vanillae*, 132; *Heliconius melpomene*, 137; *H. wallacei*, 138; *H. doris*, 139.

the insect (i.e., pre-copulation, post-copulation, before or after the rupture of the spermatophore) and due to methods of preservation and subsequent treatment. For these reasons it was found that the shape, though potentially of value,

if given homogenous material, is in practice unsatisfactory. In all species, other than some *Heliconius*, there is a strongly chitinized signum (sig.) on each side of the bursa copulatrix, whose function is assumed to be the rupture of the



TEXT-FIGS. 127-129, 133-136, 140 & 141. *Dione glycera*, 127; *D. moneta*, 128; *D. juno*, 129; *Heliconius aliphera*, 133; left signum as seen from the right side, 134; *H. isabella*, 135; *H. numata*, 136; *H. erato*, 140, *H. sara* and *H. ricini* similar; detail of interior of right signum of *P. euchroia*, 141.

spermatophore with the subsequent release of the sperm. The signa consist of a number of sharp chitinous spines (Text-fig. 141) which project into the lumen of the bursa copulatrix. The shape of the signum is reasonably constant

within species but considerable and valuable differences are apparent among species. Its value in generic classification is small, for the differences within *Heliconius* are considerably greater than those between genera like *Philaethria*, *Dry-*

adula and *Dryas* (Text-figs. 124-126), yet within *Dione* and *Podotricha* the signa of the constituent species are very similar (127-131). *Agraulis vanillae* (132) is unique in that it has a lateral vertical constriction of the bursa copulatrix which passes through the signa, and the chitinous teeth are coarser than those of any other species examined. Within *Heliconius* few conclusions can be drawn without a full survey of the genus but the signa of *H. isabella* (135) and *H. alipha* (133, 134) are more like *Dryas iulia* (126) or *Philaethria dido* (124) than any other member of *Heliconius* studied. *H. alipha* is unusual in that the signa are asymmetrical; on the right side it resembles *P. dido* and on the left *Dryas iulia*. The signa of *H. wallacei* (138) and *H. melpomene* (137) are alike and similar to *H. numata* (136), which is larger, and *H. doris* (139) which is smaller. *H. erato* (140), *H. sara* and *H. ricini* have no signa at all.

The spermatheca (Text-figs. 142-152) is prone to damage both during preservation and in dissection but it gives some characters which persist even in ill-treated material. A diverticulum is attached to the spermatheca in *Philaethria* (142), and *Podotricha* (143) by a very narrow duct, which is slightly wider in *Dryas* (144) and wider still in *Dryadula* (145), *H. isabella* (146), *H. alipha* (147) and *Dione* (148-150). In *Agraulis vanillae* (151) and the other species of *Heliconius* studied, the diverticulum is attached directly without the differentiation of a duct.

The bicornuate accessory glands (Text-fig. 93) are lined with chitin and are clearly recognizable in dried material. They appear uniform throughout the group, though due to different preservation techniques and differences in their physiological state at the time of capture, their appearance is variable.

INTERNALS

The internal anatomy of the genera available in Trinidad was examined but no features of systematic interest were recognized. The nervous system and gut are typically nymphalid. The male reproductive system exhibits a median globular testes from which two vasa deferentia emerge like the aortae of a mammalian heart, showing the fused testes have been rotated through 180°. The one specimen of *Philaethria dido* that was available for study did not show this rotation and one *Heliconius numata* out of the six examined had two separate testes. In all the species examined, a pair of accessory glands open into the vasa deferentia just proximal to the point where they join each other. The ectodermal internal female reproductive organs have been described earlier under female genitalia.

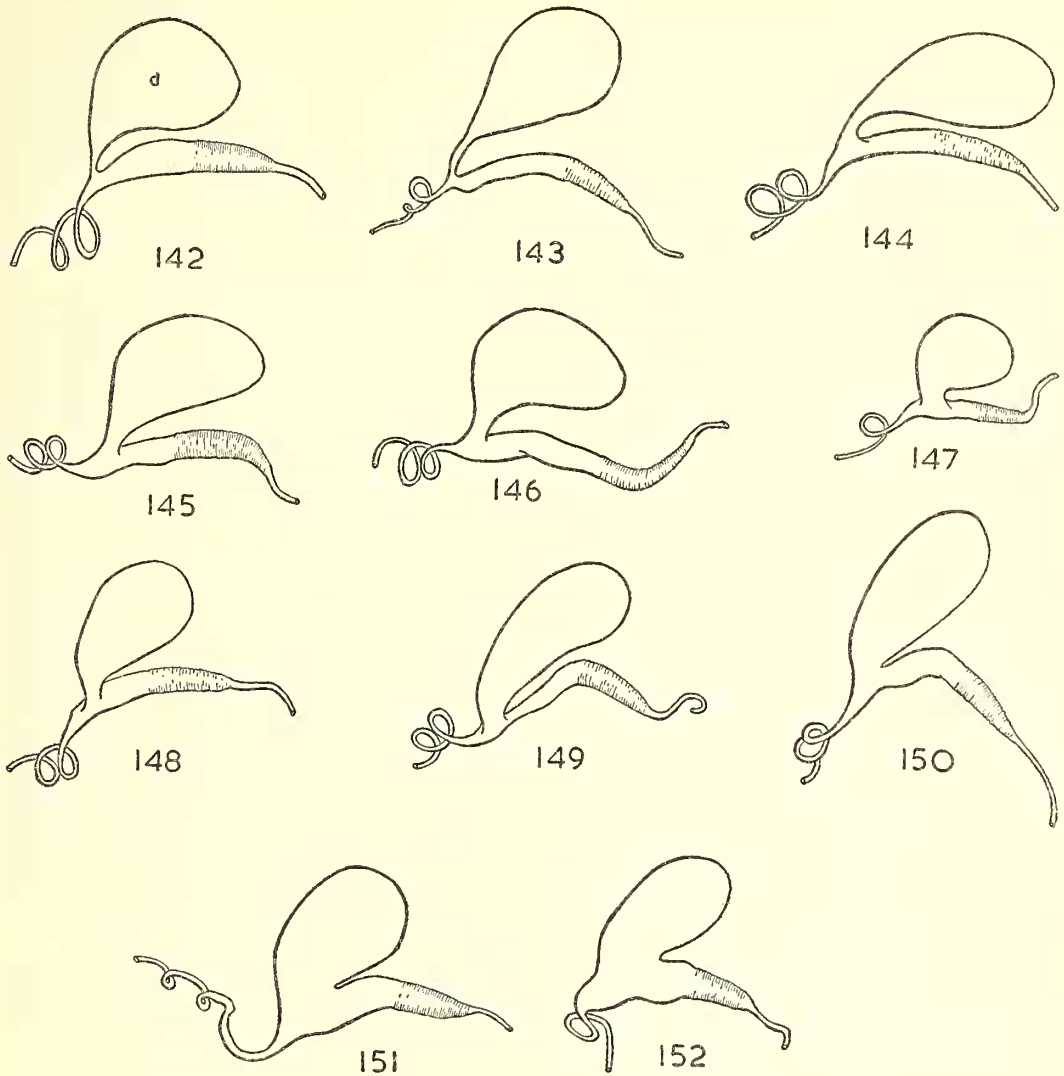
Each of the two ovaries is composed of four ovarioles.

V. DISCUSSION

Over eighty-five years ago Müller (1877a) suggested that the genera *Colaenis* (which included *Philaethria*), *Dione* (which included *Agraulis* and *Podotricha*) and *Heliconius* (which included *Eueides*) should be considered a taxonomic unit. He united these genera on many characters, some morphological and some biological involving eggs, larvae, pupae, and adults. Subsequent attempts that have been made to divide the group have been based primarily on the presence or absence of the hindwing cross-vein M2-M3 which separates off *Heliconius* from the other genera. This division does not seem any more valid than to isolate those genera in which there are androconia on the hindwing veins Sc + R1 and Rs, which would differentiate *Philaethria*, *Dryas* and *Heliconius* from the rest. Similarly, when characters other than venation and color-pattern are considered, no case can be made for species groupings such as those of Stichel (1938) who placed *Dryas iulia* and *Dryadula phaetusa* (as species of *Colaenis*) in the section Apotorneuthes, and contrasted them with *Podotricha euchroia* and *P. telesiphe* (also as species of *Colaenis*) in the section Apotomemati. However, his separation of *Dione junio* as the section Goniosimi away from the section Strongylotypici, which contained *Agraulis vanillae*, *Dione moneta* and *D. glycera* (all as species of *Dione*), is more realistic. The recognition of seven distinct genera by Michener (1942a) is reasonable and acceptable, through several generic groupings can be identified, but for which no new names are proposed.

On consideration of the characters examined in this paper, the peculiar features the adults have in common are, the recurrent Sc of the hindwing, the dorsal abdominal glands and ventral processes of females, and the wing vein androconia of males. These seem to be diagnostic group characters. Other systematic characters of value include venation, the structure and distribution of androconia, the pretarsi, the female foretarsi, the signa of the bursa copulatrix, the spermatheca and, to a more limited extent, the male genitalia. In the following discussion it will be shown that there are three generic groupings within the subfamily. Reference should be made to the family-tree (Text-fig. 153).

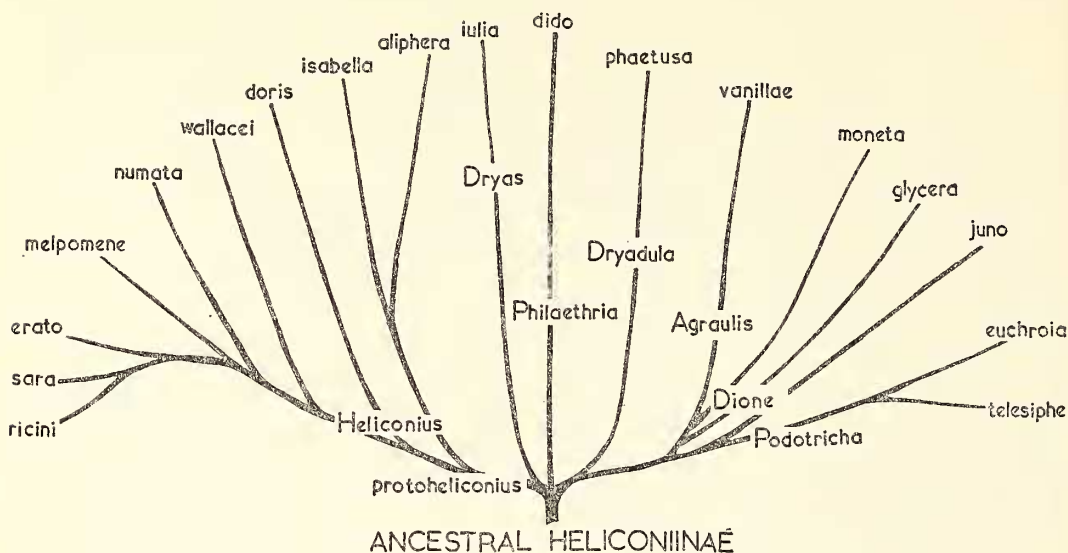
Sub-group (1): *Philaethria*, which has a unique color-pattern, has a wider distribution of wing-vein androconia than any other member of the Heliconiinae. The pretarsi and female foretarsi are typically nymphalid and apparently



TEXT-FIGS. 142-152. Heliconiine spermathecae, with the proximal portion of the spermathecal duct and the distal spermathecal gland removed; **d** is the spermathecal diverticulum. *Philaethria dido*, 142; *Podotricha euchroia*, 143; *Dryas iulia*, 144; *Dryadula phaetusa*, 145; *Heliconius isabella*, 146; *H. aliphera*, 147; *Dione juno*, 148; *D. moneta*, 149; *D. glycera*, 150; *Agraulis vanillae*, 151; *Heliconius erato*, 152.

unspecialized. The palps are the least hairy. The androconia are of the most common shape. The signa of the bursa copulatrix has both lateral and vertical limbs well developed, and is of a boomerang shape from which all the other shapes seen in the subfamily could have been derived by a differential reduction. The male genitalia show a bizarre development of the distal extremities but this is of little value in

establishing inter-generic relationships, for, as has been shown, the valves, or claspers, play no part in the prehension of the female and do not form part of a lock and key mechanism to ensure specific isolation. They have become free to exploit genetic variability to the full, for, as far as can be seen, their characters are non-adaptive. *Philaethria* should be regarded as the most conservative member of the Heliconiinae, for it ex-



TEXT-FIG. 153. Family tree.

hibits several subfamily characters in their most generalized form and has no relevant specializations.

Sub - group (2): The *Dryadula* - *Agraulis* - *Dione* - *Podotricha* group. Apart from the possession of androconia on at least six forewing veins there is no single character which unites these genera, though they may be linked in successive pairs and are more closely related to each other than to any other members of the subfamily.

Dryadula and *Agraulis* share a similarity of forewing shape though the hindwing of *Dryadula* is more rounded distally. They have a similar distribution of forewing androconia and both lack androconia on the hindwings. That these two are not very closely related is indicated by the differences in the shape of the androconia and signa, the reduction of the pretarsi and terminal spines of the female foretarsi in *Agraulis* and the absence of female abdominal processes in *Dryadula*. The male genitalia also show considerable differences, but these need not be stressed.

Agraulis and *Dione* are linked by at least the following characters: the similar pattern of silver spots on the underside of the wings and the principal elements of the upper surface wing pattern, a likeness which is reinforced by the form *A. v. lucinia*, the reduction of the meso- and metathoracic pretarsi, the reduced terminalia of the female foretarsi, the strongly capitate female abdominal processes and their hair-like bifid scales, the high degree of hairiness on the palps, the broad duct to the spermatheca diverticulum, and the elongate character of the androconia.

There are minor differences in wing shape in that *Dione* has the distal margin of the forewing more strongly emarginate and there is slight scalloping of the posterior margin of the hindwing. The principal difference is in the distribution of androconia, for *Dione* has them on some hindwing veins, but not on Sc+R1 or Rs, whereas *Agraulis* has no hindwing androconia at all. The difference in the signa is due principally to the median constriction that is peculiar to *Agraulis*. The male genitalia are distinct but this is not considered of great significance.

Within *Dione*, in addition to differences in male genitalia and signa of an order expected between distinct species, there is a considerable difference in the shape of the androconia, for *D. moneta* has androconia which resemble those of *Agraulis*, *D. juno* has androconia of more normal shape, and *D. glycera* is intermediate. This sequence is seen again in the structure of the terminal joint of the female foretarsi. However the characters of the male genitalia, signa, spermatheca and androconial distribution combine the three species of *Dione* more closely together than any one of them can be joined with *Agraulis*, though *D. moneta* seems more close to *Agraulis* than either of the other species, a relationship suggested by Stichel though without evidence.

Dione and *Podotricha* have many common characters which include wingshape, though the emargination of the forewing noticed in *Dione* is even more highly developed in *Podotricha*, and the posterior margin of the hindwing is more heavily scalloped. The distribution of the an-

droeonia is similar, though the over-all density is less in *Podotricha*, and the structure of the androconia is similar when *D. juno* is used for comparison. The pretarsi, female foretarsi, female abdominal processes and their scales are similar, though the signa of *Podotricha* is reduced in size. The male genital valves of the two species of *Podotricha* can be distinguished from each other and are substantially different from those of *Dione*.

The relationships between *Agraulis*, *Dione* and *Podotricha* are complex. On the small amount of evidence presented it seems likely that the mutual ancestor, already distinct from *Proto-Dryadula*, differentiated into two species, one of whose distinguishing characters was a tendency to have elongate androconia, and a reduction of the terminalia of the female foretarsi. Subsequently this latter group differentiated into an upland species which changed very little and still possesses the principal *Dione* characters, as *D. moneta*, and a principally lowland species which diverged markedly, losing the hindwing androconia and becoming *Agraulis vanillae*. A case could be made for returning *Agraulis* to the genus *Dione* but insufficient weight can be placed on the present evidence to warrant such a major taxonomic change. *D. glycera* is probably a conservative member of the *D. moneta* line which has retained some of the features possessed by *Proto-moneta* during its differentiation from *Proto-juno*. In addition to the androconial and female prothoracic leg characters already mentioned, *D. glycera* and *D. moneta* share the similar peculiar path of the hindwing veins Sc+R1 and M2. The two species of *Podotricha* are very close and are probably an offshoot of the *juno* side of the *Dione* bifurcation.

Sub-group (3): *Dryas* and *Heliconius* are united by the shape of the wings and the possession of similarly-arranged androconia on the hindwing veins Sc+R1 and Rs. No other genus except *Philaethria* has androconia on these veins. The lack of the crossvein M2-M3 in *Dryas* has prevented previous taxonomists from considering these two genera closely related, but not only is the distribution of androconia similar, but the structure of the hindwing androconia is similar, as are the pretarsi, female foretarsi, signa and female abdominal processes.

Heliconius can be divided into two groups, one of which can be subdivided. In the material studied, the Trinidad members of the old genus *Eueides*, that is, *Heliconius aliphera* and *H. isabella*, can be separated off from the rest on a number of characters. Their signa are alike and of the boomerang shape seen in *Dryas* and *Philaethria*, in particular the signa of *H. aliphera*

is asymmetrical and resembles *Philaethria* on one side and *Dryas* on the other. Also the androconia are similar in structure to those of *Dryas* though somewhat more squat, and as in *Dryas* occur only on the veins of the hindwing. In all the other species of *Heliconius* studied they occur on the membrane around Sc+R1 and Rs as well. *H. aliphera* has some androconia on branches of hindwing M and Cu as well as Sc+R1 and Rs, a condition which resembles *Philaethria* though *H. isabella* has them restricted to Sc+R1 and Rs. Moreover, the duct to the spermatheca is unlike that of any other species of *Heliconius* and like that of *Dryas* and *Philaethria*, in that it is narrow and not broad. Also the shape of the female abdominal processes is more pedicelate than the advanced species of *Heliconius*, a feature seen elsewhere in *Agraulis*, *Dione* and *Podotricha*. Against this evidence one must recognize in both *H. aliphera* and *H. isabella* the reduction of the female foretarsi and the peculiar shape of the paronychchia which, though they resemble the generalized pattern of *Philaethria* and *Dryas*, have spatulate tips. In view of the gross similarities among *H. aliphera* and *H. isabella* and other genera like *Philaethria* and *Dryas*, it is reasonable to assume that these two species are among the more primitive in *Heliconius*, but are not on the direct line of descent of the more highly evolved species. Hitherto these members of the old genus *Eueides* have been placed last in taxonomic lists, suggesting that they are among the most advanced, but in future, if confirmed by a more thorough study of *Heliconius*, they should be placed near the beginning.

Within the remainder of *Heliconius* there is a clear division separating *H. wallacei*, *H. doris*, *H. numata* and *H. melpomene* from *H. erato*, *H. sara* and *H. ricini*.

The first group have the following characters in common which contrast with the second group.

- (i) Dense androconia on the membrane around Sc+R1 and Rs of the hindwing. *H. wallacei* and some species (?) of *numata* that do not occur in Trinidad have androconia on branches of M and Cu on both fore- and hindwings, and in view of the possession of androconia in these positions by other genera this is probably a primitive feature. In *H. erato*, *H. sara* and *H. ricini* the androconia are only sparsely distributed over the membrane around Sc+R1 and Rs.
- (ii) The possession of a signa on the bursa copulatrix. Though these vary specifically in shape, those of *H. numata* and *H. mel-*

pomene are very much alike and differ from both *H. wallacei* and *H. doris*. There are no signa in *H. erato*, *H. sara* and *H. ricini*, but it is possible that the signa have been lost independently.

- (iii) The male genitalia have a spinose ornamentation of the elongate dorsal process of the valve, in contrast to the abbreviated rounded shape of *H. sara* and *H. ricini*, though *H. erato* resembles *H. melpomene* in that it is slightly spinose apically.
- (iv) The pretarsi have the ventral processes of the paronychial at least half as long as the dorsal processes. In *H. erato*, *H. sara* and *H. ricini* they are less than a third as long.

If these criteria are valid, then the *wallacei*, *numata*, *doris*, *melpomene* group are more primitive than the *erato*, *sara*, *ricini* group, for the *wallacei* group shows a more extensive distribution of androconia, the possession of a signa, and the almost equal development of the dorsal and ventral processes of the paronychial, which are all features seen in other genera. If this is correct, then *melpomene* is more primitive than any member of the *erato* group. Furthermore, if *melpomene* and *erato* are very closely related, as genetical research suggests, then *erato* must be the most primitive of its own group.

The relationships of the genera discussed and their constituent species, within the limits of this paper, are represented by a family tree in Text-fig. 153.

Heliconius is undergoing a rapid, or, as Beebe, Crane & Fleming (1960) describe it, an explosive evolution, giving rise to a large number of recognizable forms, some of which are biologically good species but many of which are not. The taxonomy of *Heliconius* has been complicated in the past by failure to recognize the significance of polymorphism and mimicry and by the use of characters which do not expose similarities due to convergence. The characters used in this paper, when applied to *Heliconius* as a whole, should help considerably to sort out the chaos in which the genus is at the moment.

VI. CONCLUSIONS

- (1). The Heliconiinae is a natural group and Michener's (1942a) division into seven genera is reasonable and acceptable.
- (2). The taxonomic characters used in this paper, which include the female foretarsi, the pretarsi, the venation, the androconia and their distribution, the female abdominal processes, the signa of the bursa copulatrix, the spermatheca and the male genital valves,

are useful and applicable both to dried and fresh material.

- (3). There are three principal divisions to the subfamily:
 - (a) A central stem contemporarily represented by the conservative *Philaethria*.
 - (b) A diverse group containing *Dryadula*, which is the most distinct genus, and *Agraulis* and *Dione* and *Podotricha* which are closely related.
 - (c) *Dryas* and *Heliconius*, of which *Dryas* is the single living representative of the common stem from which *Heliconius* has evolved.
- (4). *Heliconius* is in need of revision using valid criteria, but upon the examination of the nine species that occur in Trinidad there seem to be two principal divisions. One which contains *H. aliphera* and *H. isabella* (members of the old genus *Eueides*), which are primitive, and the rest, which seem also capable of division into the *wallacei*, *doris*, *numata*, *melpomene* group which is probably older than the *erato*, *sara*, *ricini* group.

VII. SUMMARY

The morphology of the Heliconiinae is described where relevant to the systematics of the subfamily. All the species of the genera other than *Heliconius* are included, but within *Heliconius* material was confined to the nine species available in Trinidad.

An interpretation of the evolutionary relationships within the subfamily is suggested, based upon the examination of characters which include the pretarsi, the female foretarsi, the venation, the structure and distribution of androconia, the signa, the spermatheca, the female abdominal processes and the male genital valves.

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PLATE I

Imagos of Heliconiinae from Trinidad. All the species are illustrated in color in Seitz: *Macrolepidoptera of the World*; the American Rhopalocera, Vol. V, Plates (1924).

- FIG. 1. *Dione juno*.
FIG. 2. *Agraulis vanillae*.
FIG. 3. *Dryadula phaetusa*.
FIG. 4. *Dryas iulia*.
FIG. 5. *Philaethria dido*.
FIG. 6. *Heliconius isabella*.
FIG. 7. *Heliconius alipha*.
FIG. 8. *Heliconius melpomene*.
FIG. 9. *Heliconius numata*.
FIG. 10. *Heliconius erato*.
FIG. 11. *Heliconius ricini*.
FIG. 12. *Heliconius sara*.
FIG. 13. *Heliconius wallacei*.
FIG. 14. *Heliconius doris*.